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Components of reaching and grasping an object may emerge following a single minimization process

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Director : Dr. Anatol G. Feldman

Mémoire présenté à la Faculté des études supérieures
en vue de l'obtention du grade de maîtrise
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Ce mémoire intitulé :

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présenté par :
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A été évalué par un jury composé des personnes suivantes :
Daniel Bourbonnais, président-rapporteur
Anatol G. Feldman, directeur
Joyce Fung, membre du jury

Résumé

Bien que l'atteinte et la préhension d'un objet puissent être décomposées en plusieurs éléments, incluant le transport de la main et la saisie de l'objet, nous avons évalué l'hypothèse selon laquelle les différents éléments du mouvement ne sont pas préprogrammés par le système nerveux central. Ces différents éléments émergeraient plutôt d'un seul processus qui tendrait à minimiser la distance et la différence de forme existant entre la surface de la main de référence, telle que modifiée par le cerveau pendant le mouvement, et la surface réelle de la main. Les différentes composantes du mouvement et la surface réelle de la main émergeraient selon ce processus de minimisation, en tenant compte des interactions centrales et réflexes des éléments neuromusculaires, ainsi que des forces externes agissant avant et pendant la saisie de l'objet. Ainsi, ces éléments se comportent en un ensemble cohérent guidé par le processus de minimisation afin d'atteindre le but moteur. L'hypothèse qui a été testée est que les perturbations mécaniques qui retardent l'exécution d'une composante du mouvement pourraient donc retarder l'apparition des autres composantes. Nous avons ainsi examiné l'implication de cette hypothèse de minimisation. Après un signal sonore, des sujets assis ont déplacé leur main droite (dominante) pour atteindre et saisir un objet (cube) placé dans l'espace de préhension (expérience 1) ou au-delà (expérience 2, distance supérieure à la longueur du bras). Dans l'expérience 2, le sujet devait, en plus de bouger son bras, déplacer le tronc vers l'avant afin d'atteindre et de saisir l'objet. La vision du sujet a été bloquée simultanément avec le signal sonore (spécifiant le moment pour débuter le mouvement). Le mouvement du poignet ou du tronc (selon la tâche) a été bloqué par un dispositif électromagnétique, à différentes phases du mouvement et pendant des durées variables, tel que spécifié par le programme dans 30% des essais choisis de façon aléatoire (ordre des essais inconnu du sujet). Lorsque le mouvement du poignet a été mécaniquement bloqué (expérience 1), les

changements dans l'ouverture de la main amorcés au début du mouvement ont cessé et sont retournés à la normale seulement après que le poignet eut été libéré de la contrainte mécanique. En variant le temps du début de la perturbation et sa durée, il a été possible d'arrêter ces changements dans n'importe quelle phase du mouvement, même lorsque les doigts commençaient à fléchir pour saisir l'objet. Des influences similaires ont également été observées lorsque le mouvement du tronc a été bloqué pendant la tâche où l'objet était placé plus loin que la longueur du bras du sujet (expérience 2). Cependant, lorsque le mouvement du tronc était interrompu par la perturbation, ceci n'affectait pas le transport de la main jusqu'à l'objet, à moins que le tronc n'ait été bloqué après l'extension maximale du bras. Le fait que l'ouverture de la main puisse être interrompue à n'importe quelle phase par le blocage du mouvement du poignet ou du tronc concorde avec l'hypothèse de minimisation. La même hypothèse sert à expliquer que la rétention du tronc dans l'expérience 2 a influencé l'ouverture de la main mais pas le transport de la main. En effet, il a été démontré que la contribution du déplacement du tronc aux mouvements de la main visant un objet situé plus loin que la longueur du bras est initialement neutralisée par des changements compensatoires dans les angles articulaires du bras, et ce, jusqu'à ce que le bras atteigne son extension maximale. Par conséquent, le blocage du tronc avant ce moment n'influencerait pas le transport de la main. Par contre, les changements dans l'ouverture de la main ont montré une forte dépendance sur la possibilité qu'avait le tronc d'apporter la main vers l'objet, puisque le blocage du mouvement du tronc a arrêté les changements dans l'ouverture de la main. En conclusion, nos résultats ont montré que les changements dans l'ouverture de la main peuvent être interrompus à n'importe quelle phase du mouvement si on arrête le mouvement du tronc ou du poignet, ce qui concorde avec l'hypothèse de minimisation développée par Gelfand et Tsetlin (1971, principe de l'interaction minimale).

Mots clés: perturbation mécanique, blocage du bras, blocage du tronc, composante de transport de la main, composante de l'ouverture de la main, contrôle de la position-seuil, contrôle moteur.

Abstract

We hypothesize that, although reaching and grasping an object can be seen as consisting of several components, including the hand transport and grasping the object, they are not preprogrammed by the nervous system. Instead, they emerge following a single process that tends to minimize the distance and difference in shapes between the referent hand surface modified by the brain and the actual hand surface (the minimization rule). Different movement components and the actual hand surface emerge following this minimization process constrained by central and reflex interactions of neuromuscular elements between themselves and with external forces acting before and during grasping the object. These elements thus behave together, as a coherent ensemble guided by the minimization process in achieving the motor goal. Mechanical perturbations that delay the performance of one movement component may postpone the appearance of other components. We tested this implication of the minimization hypothesis. In response to a sound signal, seated subjects moved the right (dominant) hand to reach and grasp an object (cube) placed within (experiment 1) or beyond (experiment 2) the reach of the arm. In experiment 2, subject not only moved the arm but also bended the trunk forward to reach and grasp the object. The vision was blocked simultaneously with the signal to move. In 30 % of randomly selected trials, the wrist or trunk motion in the respective experiments was prevented by an electromagnetic device at different phases of motion, for different periods of time. When wrist motion was mechanically blocked (experiment 1), changes in the hand aperture ceased and resumed only after the wrist was unblocked. By varying the onset time and duration of perturbation, it was possible to cease these changes at any phase of motion, even then fingers began to close on the object. Similar influences on the hand aperture were observed when trunk motion was blocked in movements beyond the arm's reach (experiment 2). Preventing the trunk motion, however, did not influence the hand transport to the

object, unless the trunk block was initiated after the arm reached its extension limits. The finding that changes in the hand aperture can be interrupted at any phase by arresting the wrist or trunk is consistent with the minimization hypothesis. The same hypothesis helps explain why the trunk arrest in experiment 2 influenced the hand aperture but not the hand transport. It has been previously shown that the contribution of trunk motion to the hand movement extent in motion beyond the reach of the arm is initially neutralized by compensatory changes in the arm joint angles until the arm reaches its extension limits. Therefore, trunk arrest prior to this moment could not influence the hand transport. In contrast, changes in the hand aperture critically depended on whether or not the trunk motion could eventually bring the hand to the object, such that preventing the trunk motion discontinued the aperture changes. In conclusion, the finding that the changes in the hand aperture can be interrupted at any phase by arresting the wrist or trunk is consistent with the minimization hypothesis.

Keywords: mechanical perturbation; arm arrest; trunk block; hand transport component; hand aperture component; threshold position control; motor control.

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List of abbreviations

CNS : central nervous system

EMG: electromyographic activity

EP: equilibrium point

IC : invariant characteristic

RTG : reach to grasp

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CHAPTER I

1.0 Introduction, review of literature and objectives

1.1 Introduction

Reach-to-grasp (RTG) movement is an everyday action controlled by the nervous system depending on the choice of the object, its size, shape, location, and orientation. It consists of several, functionally different components, including the transport component bringing the hand towards the object, and the grasp component that includes adjusting the hand configuration according to the object's shape and orientation and making an appropriate hand aperture (opening phase) before closing fingers on the object (closure phase). Reaching may involve motion of the trunk or even the whole body, for example, when the object is placed beyond the reach of the arm. It has been suggested that the transport and grasp components of RTG movements are pre-planned as separate units coordinated by a loose temporal coupling (Jeannerod, 1981, Jeannerod et al., 1984; Jeannerod et al., 1995; Paulignan et al. 1991, Hoff and Arbib 1993). Here, we hypothesize that all body segments involved in RTG movement are governed as a single coherent unit following a global minimization process associated with the necessity to reach the motor goal, whereas different movement components emerge following this global factor without any pre-preplanning (Berkinblit et al. 1986; Feldman et al. 2007; Smeets and Brenner 1999). We predicted that by arresting arm or trunk motion during RTG movements, one can interrupt the

minimization process and, as a result, interrupt the changes in the hand aperture, until the arrested segments are released. Since the minimization process is gradual, the changes in the hand aperture can be interrupted practically at any time, not only during the opening but also closing phase. We tested this prediction in the present study.

1.2 Review of literature

In this study we addressed the question of how the nervous system controls movements consisting of several motor components. We review the literature that addresses this question. With the specific attention to studies of reach-to-grasp (RTG) movement and then to the description of the minimization rule that presumably underlies the control of these movements.

1.2.1Reach to grasp movement

In our everyday life, reach to grasp movement is one of the most frequent actions. This action is not as simple as it may seem. Reach-to-grasp (RTG) movements have been well described within the research literature since the pioneering work of Jeannerod (1984). RTG movements provide a powerful tool for examining how the human nervous system organizes movements (i.e. they offer a microcosm of normal motor control behaviour). RTG movements is useful for studying issues related to motor control because the behavior shows certain invariant characteristics (see Jeannerod 1984). For example, the wrist movement

has a smooth, approximately 'bell-shaped', speed profile. The wrist accelerates to a maximum speed and then decelerates as the object is approached. RTG movement consists of several, functionally different components, including the transport component bringing the hand towards the object, and the grasp component that includes adjusting the hand configuration according to the object's shape and orientation and making an appropriate hand aperture (opening phase) before closing fingers on the object (closing phase). The invariance of RTG movements provides a tool for exploring changes in behavior following perturbation of the environment.

Nonetheless, the description of prehension movement does not lack controversy. The controversy arises because different theoreticians have different conceptions of how movements are organized. Rules and mechanisms governing the coordination between the movement components are not completely understood. Specifically, two issues are still in debate. First, whether the transport and grasp components are controlled as a single unit or separately. Second, whether the transport and grasp components are coordinated based on temporal or spatial information of the movement is still in debate.

1.2.1.1 Interdependence of RTG movement components

In an attempt to understand how the nervous system coordinates such complex movements, many researchers have investigated the relationship between the hand transport and hand grasp components and have proposed several mechanisms underlying the coordination between the different components.

It has been originally suggested that the grasp and transport components are governed by independent visuomotor channels, which are synchronized by a loose temporal coupling (Jeannerod, 1981, Jeannerod et al., 1984; Jeannerod et al., 1995). Jeannerod et al. have observed that a maximum in grasp size occurs in relatively fixed temporal relationship with the transport component. He hypothesized that transport and grasp components of RTG movements are pre-planned as separate units centrally patterned and that they do not depend on feedback from the current movement (Jeannerod et al., 1984; Jeannerod et al., 1995). They showed some evidence including experimental and clinical observation (Jeannerod et al. 1994, 1995, Paulignan et al. 1991a, b). Further, this idea of independent control between the transport and grasp components has received support from recent anatomical and physiological work showing distinct cortico-cortical pathways for reaching and grasping. Jeannerod and colleagues did experiments showing that changes in object attributes, affect only grasp, and not characteristics of transport (Paulignan et al. 1991a, b). There is also a clinical case supporting this point of view: a patient (A.T.) with a bilateral posterior parietal lesion of vascular origin presented a bilateral deficit in grasping simple objects without deficit in reaching toward the location of these objects (Jeannerod et al. 1994).

The hypothesis of independent visuomotor channels can be tested by perturbing one component and looking for a coordinated response to the perturbation in the second component. If the channels are independent, perturbing one channel should not affect the other. On the other hand, if they do share information, one would expect both a response in the perturbed effector and an adjustment in the other channel to maintain the desired state-space coordination between the two components. Haggard and Wing (1991, 1995) used mechanical perturbations to pull the arm backwards or push it forwards towards the target during movement. They found that effective pulling perturbation caused a hand

transport reversal, trials showing this hand reversal also showed an aperture reversal. The response of hand aperture to the perturbations appeared to maintain the spatial relation between the two components. Across all subjects, a fixed delay occurred on the reversals after the perturbation. The hand transport reversal typically occurred around 12 ms after the onset of the perturbation, and the hand aperture reversal occurred some 70 ms later. These spatial and temporal relationships confirmed their hypothesis that hand transport and aperture are interdependent.

The studies described above involved tasks of reaching for an object by only extending the arm. In daily life, however, individuals are confronted with situations where an object is located beyond the arm's reach, so the trunk becomes involved in the arm transport to extend the reach. In such a situation, the motor control system needs to not only control the grasp and transport components, but also coordinate the trunk with the arm.

Wang and Stelmach (1998) have shown results of their experiments where the subjects were asked to reach and grasp an object using the arm only, the trunk only, and combinations of both arm and trunk. Despite the fact that differences in the relative time to peak velocity of both the arm and the trunk motions were statistically significant across conditions, the relative time to peak velocity of the endpoint motion was not, indicating that the endpoint velocity profiles are consistent regardless of whether or not the trunk or arm are involved in the movement. This finding confirms that of Ma and Feldman (1995) that endpoint trajectory remained invariant regardless of the direction of the trunk movement (forward or backward) and regardless of whether or not that trunk motion was blocked. They suggested that the grasp and transport components are governed by two independent neuromotor synergies, which in turn are coordinated at a higher level. In a later study of Wang and Stelmach (2001), three factors were changed across trials of reaching and grasping involving trunk movements: movement

amplitude (near and far), object size (either 1 or 38 mm in diameter), and reaching speed (slow and fast). Invariance in closure distance was observed across all situations, regardless of whether the coordination between the grasp and the transport components was influenced by the involvement of body segments (i.e., arm only, trunk only, or both) or by the changes in movement amplitude, reaching speed, and object size. Wang and Stelmach stated that the arm and trunk motions, which are governed by separate neuromotor synergies, are functionally unitized by a higher-order synergy as an overall transport component to accomplish the goal of reaching; in turn, this overall transport component is coordinated with the grasp component by another higher-order synergy to accomplish the global goal of reaching and grasping.

1.2.1.2 Spatial and temporal coordination between RTG components

Even after numerous studies of prehensile movements, the questions remains as to whether the transport and grasp components are coordinated based on temporal or spatial information of the movement.

Jeannerod (1984) had shown a temporal coupling between two components and argued that the temporal link between two components is centrally patterned and does not depend on feedback from the current movement.

Paulignan et al. (1991) did experiments where the object position or size was changed at the onset of the movement. Their results of this changes in object position showed that the spatial wrist paths first diverged during the initial part of the trajectory, and later converged to the object location that had been perturbed. The point in time where the paths began to converge was located approximately at the time of the peak velocity of the wrist. They suggested the control mechanisms

of transportation might be separated in two parts, with responses to acceleration and deceleration phases respectively.

Furthermore, Hoff and Arbib (1993) advanced a quantitative model targeting much of the data on temporal coordination. Their model posits that maximum aperture is synchronized with the temporal ending of the reaching movement. The coordination is based on maintaining a consistent enclosure time (approximately 200 ms). Thus, Hoff and Arbib (1993) developed a temporal coordinator model showing that two components are not independent of each other and that they are coordinated by a certain temporal mechanism.

However, some reports of Jeannerod and colleagues indicated the spatial interdependence between these two components. For example, they reported an experiment where the objects (plastic cylinders) widely distributed in the workspace along a circle centered on subject's head axis, starting from 10° on the left from the sagittal axis, up to 40° on the right (Paulignan et al.1997). Objects position not only affected the duration and the kinematics of the hand transport component but also influenced the grasp component. The amplitude of aperture was larger for an object of the same size when it was placed on the right side (and thus at a shorter distance from the hand resting position) than when it was placed on the left side of the display. By contrast, the other results showing that grip size tends to increase with object distance in the sagittal plane (Jakobson and Goodale 1991; Chieffi and Gentilucci 1993). Possibly, increasing object distance in each direction would yield an increase in maximum grip aperture. Movements in different directions involve different combinations of joint rotations. A movement directed at the leftmost object involves shoulder adduction and elbow extension, whereas a movement directed at the rightmost object involves shoulder abduction and moderate elbow extension.

The grasp component and rotation of the hand can be describe by vectors (see also Paulignan et al. 1997). This method was used by several authors (Napier 1955; Iberall et al.1986; Carey et al. 1996; Gentilucci et al. 1996; Paulignan et al.1997). The position of the tips of the thumb and index finger was sampled and the opposition axis was defined as the line connecting those tips. Paulignan et al measured this orientation with respect to different reference frames originatingthe tips of the two fingers. from the object center (object-centered frame, which used the *Y* axis as the reference for calculating the angle of orientation of the opposition axis) or from a body part (body-centered frame, the line connecting the center of the head and the object center as the reference axis). The orientation of the opposition axis was invariant, when this measure was made at the end of the movement with respect to a body-centered reference. The forearm and hand were displaced optimally regardless of object location. This was achieved by combined rotations at the shoulder joint (for matching the object location in azimuth) and the elbow joint (for matching the object distance from the body).

Alternatively, Wing and colleagues (1986, 1991, 1995, 1998) have found a systematic relationship rather than a temporal coupling between the hand transport and aperture components. Wing et al. (1986) reported that changes in maximum size of grasp aperture are associated with changes in spatial accuracy of transport. In their experiment, the RTG movements were produced in three situations: normal reaching, fast reaching (subjects reached for the dowel as fast as possible) and blind reaching (subjects closed eyes after the dowel had been repositioned). The result showed maximum apertures in three situations were significantly different. The aperture associated with fast reaching was 13 mm greater than that in normal reaching, while the aperture for blind movement was 35mm greater than normal. Thus, changes in maximum aperture accompany changes in the accuracy of the transport component in reaching.

Haggard and Wing (1991, 1995) pulled back the upper right arm during the first 560 ms of the RTG movements and found coordinated responses in the hand aperture component. Effective pulling perturbation caused reversals in both hand transport and aperture reversal. When hand aperture is plotted against hand transport, the reversals of hand transport and hand aperture produced a visually striking loop in the plot. Bigger perturbations affected the hand transport and increased the hand aperture, to preserve the spatial relation between the two. Haggard and Wing (1995) proposed a simple model of this spatial coordination based on the finding that the aperture magnitude remains invariant during the grasp regardless of perturbation.

This notion of the state-space coordination has been supported by their later experiment (Haggard and Wing 1998) in which subjects had to pass over a "via point" marked on the work surface before picking up an object in the target location. It was investigated if hand aperture coordinates with the spatial path of the hand transport by comparing straight prehensile movements with curved movements. By calculating the delay in hand opening (the displacement from the start to the point at which the hand aperture exceeded its initial value in that movement by 1 cm), they found a significantly different effect on the aperture opening delay when they compared between the straight and the curved condition. Spatial plots of hand aperture against hand transport showed that the pre-shaping of the hand to prepare an appropriate grasp was delayed in the curved movements relative to the straight movements. Most of the pre-shaping of the hand occurred after passing the via point, even when the via point occurred late in the course of the movement. This delay in hand opening shows both spatial and temporal coordination in prehensile movement. First, the hand transport spatial information (straight or curved via point) is used for the control of hand aperture. Second, it also has important consequences for theories of temporal coordination, since this difference in hand opening delay also can be considered as a temporal difference

between two conditions. However, this assumption is inconsistent with a common synchronization signal to start the hand aperture and hand transport channels simultaneously (Jeannerod 1981, 1984).

Recent studies have provided support for the state-space notion of coordination (Haggard and Wing 1995; Wang and Stelmach 1998, 2001; Saling et al. 1998; Rand et al. 2004, 2006, 2007; Alberts et al. 2000, 2002). Specially, invariance in closure distance (the peak aperture occurred at approximately the same point in distance between the initial and object positions, across conditions, when it was plotted against normalized hand-transport distance) was observed while the temporal parameters of two components varied significantly across different conditions. The conditions were changed by the involvement of body segments (i.e., arm only, trunk only, or both) or by the different amplitude of movement, transport speed, and object size, or by the alterations in transport path (i.e., reaching an object over an obstacle or via point). These findings confirmed the hypothesis that aperture-closure distance is a stable variable controlled by the nervous system (Haggard and Wing 1995; Wang and Stelmach 1998, 2001; Saling et al. 1998; Rand et al. 2004, 2006, 2007; Alberts et al. 2000, 2002).

1.2.1.3 Effects of mechanical perturbations applied to RTG movements in previous studies

The experimental method used in this work addresses a more general issue in motor control, since it investigates whether two effectors can be coordinated by using information about the state of one effector in the control of a second, especially in the RTG movement which must be continuously monitored and controlled by the motor system. But most studies perturbed at the onset of the

movement by changing the object size or position, or by changing the trajectory with an obstacle (Paulignan et al. 1991, 1997; Saling, et al. 1996; Saling et al. 1998; Timmann et al. 1996). No studies utilized perturbations applied to one movement component randomly during its course without affecting other components. This is important because it would allow one to demonstrate whether if the two movement components are consistently interdependent during the movement or only during a specific period (e.g., during aperture closure).

For example, Haggard and Wing's (1991, 1995) applied perturbations during the movement as following: an electric actuator comprising a torque motor connected to a ball screw was attached to the upper right arm with a cuff. In normal operation, the force delivered by the actuator was controlled so as to be equal and opposite to the force measured by a force transducer located between the actuator and the cuff around the arm. This arrangement ensured that there was no net force acting on the subject's moving arm, provided subject moved at a moderate speed (up to 30 cm/s). The force was chosen to be a pull or a push of 5, 10, 15 or 20 N. Perturbations were delivered at a random interval of between 1 and 560 ms after the start of the trial. The amount of vertical movement was in any case restricted by the actuator cuff, so that subjects were required to reach and grasp the object directly in front of the initial position, with a trajectory compatible with the actuator's attachment. Additionally, subjects were instructed to transport at a certain speed range, being counteracted to move slowly because of the constraints in the actuator which was always at its full speed. Haggard and Wing's mechanical perturbation was advantageous in two ways. First, the perturbation was applied during active, goal-directed movement. Second, the perturbations were delivered to just one of the participating effectors, intermediate in the proximal-distal chain. However, In Haggard and Wing's experiment, trajectory and velocity of the movement are both constrained to be compatible with the actuator's moving direction and speed. This suggests that subjects could not perform a normal comfortable RTG movement. Strongest pull (around 20 N)

perturbation caused the greatest disruption of the hand transport. These strong pull perturbations were effective to make reversals in hand transport as well as in hand aperture. The looped hand aperture plotted against hand transport was only produced by the strongest pull perturbation. These responses of hand aperture appeared to maintain a spatial relationship between two RTG movement components. Weak pull perturbations and push perturbations were generally not noticed by the subject.

Effects of another mechanical perturbation applied during RTG movement were reported in experiments by Rand et al. (2004). An elastic load acted on the wrist at an angle of 105° lateral to the reaching direction in chosen trials. Perturbations were applied first on successive trials (predictable perturbations) and then randomly selected trials (unpredictable perturbations). The elastic perturbations were applied to the arm throughout the reach, and the load was increased as the reach progressed. This study focused on how reach-to-grasp movements are modified during adaptation to external force perturbations applied on the arm during reach. In the early predictable perturbation trials, reach path length became longer and reaching duration increased. As more predictable perturbations were applied, the reach path length gradually decreased and became similar to that of control trials. The maximum size of hand aperture initially increased in response to perturbations. During the course of learning, it also slightly decreased but not returned to that of control trials. Throughout unpredictable perturbation trials, large grip aperture values were observed. In addition, the spatial location where the onset of finger closure occurred showed minimum changes with perturbation. The aperture closure distance appeared to be maintained regardless the predictable or unpredictable perturbations.

Even though mechanical perturbations were utilized in previous studies, there are still issues to resolve. It was necessary to improve the mechanical device

in order to achieve a perturbation applied to the arm at a random phase throughout a normal comfortable RTG movement for a randomly selected duration.

1.2.1.4 Compensatory arm–trunk coordination

When an object is located beyond the arm's reach, the trunk becomes involved in the arm transport to extend the reach. In such a situation, the motor control system needs to not only control the transport components of the moving arm, but also coordinate the trunk with the arm. Compensatory arm-trunk coordination is produced, basing on two control strategies that have been proposed (Pigeon & Feldman 1998). First, the compensatory arm movements may be guided by control signals that simultaneously produce the trunk motion. Second, the compensation may be guided by proprioceptive and/or vestibular afferent signals elicited by the trunk motion and transmitted to the arm motor system. Proprioceptive systems may influence posture and movement at segmental levels, via ascending pathways involved in trans-cortical reflexes (Jankowska 1992) or by conveying an efference copy of central control signals combined with peripheral afferent signals (e.g. Orlovsky et al. 1999).

Recent studies showed that the hand trajectories of pointing movements to targets within arm's reach remain invariant when subjects intentionally flex the trunk or when the trunk motion is unexpectedly prevented by an electromechanical device (Adamovich et al. 2001; Ma and Feldman 1995). The trajectories remain invariant even if the hand movements are produced to remembered targets, i.e., in the absence of vision (Pigeon et al. 2000). When the trunk is moving, the influence of trunk motion on the hand trajectory is minimized by appropriate compensatory modifications of the arm joint angles, compared

with the situation when the trunk is motionless (Adamovich et al. 2001). These angular modifications in trunk assisted reaching are called compensatory arm movements or compensatory arm–trunk coordination. When trunk motion is either free or blocked in randomly occurring trials, the invariance of hand trajectory is maintained by using or excluding the compensatory coordination, respectively. Although the absence of vision leads to an increase in movement error, the basic characteristics of compensatory arm-trunk coordination during reaching are preserved (Pigeon & Feldman 1998; Pigeon et al. 2000).

In study of Rossi et al. (2002), sitting subjects made fast pointing movements towards target placed beyond the reach of arm so that a forward trunk motion was required to assist in transporting the hand to the target. In randomly selected trials, the trunk motion was unexpectedly prevented by an electromagnet. Subjects were instructed to make stereotypical movements whether or not the trunk was arrested. In non-perturbed trials, most subjects began to move the hand and trunk simultaneously. In trunk-blocked trials, hand trajectory and velocity profile initially matched those from the free trunk trials, approximately until the hand reached its peak velocity. The arm inter-joint co-ordination substantially changed in response to the trunk arrest at a minimal latency of 40 ms after the perturbation onset. When pointing is produced to targets beyond the arm's reach, the influence of the trunk motion on the hand trajectory is initially fully compensated, but when the arm approaches the reaching limits, the gain of the compensatory coordination is attenuated, allowing the trunk to contribute to the hand movement extent and direction (Rossi et al. 2002). Adamovich et al. (2001) addressed the question of whether the compensatory arm–trunk coordination relies on an anticipatory strategy by making modifications of arm joint angles depending on the prediction of the presence or absence of trunk motion in the approaching trial. They analyzed trunk-assisted pointing movements to targets placed within arm's reach. The trunk motion was prevented in comparatively rare and randomly selected trials. In this situation, the anticipatory strategy would be

ineffective because of the high probability of errors in anticipation and, as a consequence, frequent movement errors. Subjects had no difficulty in maintaining the same hand trajectory regardless of the trunk condition, implying that the compensatory coordination in trunk-assisted reaching may not rely on anticipation. Adamovich et al. (2001) also found that centrally programmed compensatory reactions triggered online (i.e., when the trunk moves during the current trial) would be too late to account for the invariance of the hand reaching trajectory. Thus neither anticipatory nor triggered compensatory central commands, but rather sensory (proprioceptive, cutaneous, and/or vestibular) feedback resulting from trunk motion may underlie the compensatory modifications in arm joint angles that maintain the same hand trajectory despite changes in the number of degrees of freedom involved in the pointing task. Rather, it was found that signals evoked by the vestibular system and descending through the vestibulo-spinal and reticulospinal pathways would play a major role in adjusting the compensatory coordination to achieve the invariance of the reaching trajectory (Raptis et al, 2007) in conditions where the trunk involvement varies.

After a review of literature on RTG movements, we will focus on the minimization rule that implies that the nervous system tends to minimize the distance to the object and the difference in shapes between the referent hand surface modified by the brain and the actual hand surface, which presumably underlies the control of these movements, as well as on the notion of threshold control on which the minimization rule is based.

1.2.2 Minimization rule

Any difference between the system's threshold and actual position elicited by threshold resetting causes an increase in the activity of neuromuscular elements and interactions between them and the environment. Gelfand and Tsetlin (1971) suggested that the response of neuromuscular elements to any imposed activity and interactions, whether elicited by reflexes or central control influences, is guided by the *principle of minimal interaction*: the connections between different neuromuscular elements are organized in a way that allows them to act as a coherent unit and reduce the imposed activity and interactions as much as possible. The principle of minimal interaction may underlie the functioning of not only executive define but also control levels responsible for resetting the threshold position: the difference between the positions of effectors from the desired position defined by the motor goal may force the control levels to adjust the threshold positions at these and subordinate levels in order to diminish the difference. The values of individual muscle thresholds (λ-s) of numerous muscles emerge following minimization of the neuromuscular activity evoked by changes in the referent body configurations.

Specific definitions of the minimization process and spatial controller presumably underlying not only reach to grasp (RTG) movements but also other motor actions have recently been proposed in an advanced formulation of the equilibrium-point hypothesis (Feldman et al. 2007; Pilon et al. 2007). This formulation is based on the finding that the nervous system is capable of setting the threshold (referent) position of the body or its segments (Asatryan and Feldman 1965; Feldman and Levin 1995; Archambault et al. 2005; St-Onge and Feldman 2004; Foisy and Feldman 2006; Feldman et al. 2007). In the referent position (R), muscles are silent but are prepared to generate activity and forces in proportion to the deviation and rate of change of the actual position (Q) from R. To produce an intentional arm movement, the system changes the referent arm position in a task-specific way. The initial arm position thus becomes the position

that deviates from the newly specified threshold position. As result, motoneurons of some muscles appear to be in a supra-threshold state and produce EMG signals and muscle forces that drive the arm away from the initial position. The whole process is guided by a minimization rule – the tendency of neuromuscular elements acting individually and collectively to diminish the gap between the Q and R. The movement continues until the gap between the Q and R is either fully eliminated (in the absence of opposing or assisting external forces) or diminished to a degree such that the residual muscle activity gives rise to forces just sufficient to counterbalance the external forces. In other words, by specifying a referent position, the nervous system sets the spatial boundaries in which neuromuscular elements are allowed to work. In this spatial frame, neuromuscular elements act as a coherent unit due to mechanical, reflex and central interactions between themselves and with the environment. Eventually, they reduce the imposed activity and interactions as much as possible, in the limits defined by biomechanical and environmental constraints, including the requirement to reach the motor goal. The minimization rule has been illustrated by successful simulations of arm movements with an anticipatory increase in the grip force (Pilon et al. 2006) and sit-to-stand movements in humans (Feldman et al. 2007).

1.2.3 Basic concepts of Threshold control

Movement production can be described by two hierarchically related sets of variables (Feldman 1986; Latash 1993; Feldman and Levin 1995). One set consists of kinematic and kinetic *variables characterizing the motor output* of the system (e.g. the trajectory of the effector, position and velocity of body segments, muscle forces and torques). These variables depend on the external mechanical conditions and perturbations. The other set of variables consists of *control*

variables. These are the internal variables that the nervous system may use to influence output variables even if the external conditions remain unchanged. In some motor tasks, control variables may remain invariant despite mechanical perturbations influencing the motor output (Asatryan and Feldman 1965).

The static component of the torque-position relationship is referred to as the invariant characteristic (IC). Control systems produce movements by changing the activation thresholds and thus shifting the IC of the appropriate muscles in joint space. This control process upsets the balance between muscle and external torques at the initial limb configuration and, to regain the balance, the limb is forced to establish a new configuration or, if the movement is prevented, a new level of static torques. Thus by shifting the IC, control systems reset the EP(equilibrium point). The study of Ghafouri and Feldman (2001) evaluated the duration of the IC shifts underlying fast point-to-point arm movements. Subjects made fast (hand peak velocity about 1.3 m/s) planar arm movements toward different targets while grasping a handle. Hand forces applied to the handle and shoulder/elbow torques were, respectively, measured from a force sensor placed on the handle, or computed with equations of motion. In some trials, an electromagnetic brake prevented movements. In such movements, the hand force and joint torques reached a steady state after a time that was much smaller than the movement duration in unobstructed movements and was approximately equal to the time to peak velocity (mean difference <80 ms). In an additional experiment, subjects were instructed to rapidly initiate corrections of the pushing force in response to movement arrest. They were able to initiate such corrections only when the joint torques and the pushing force had practically reached a steady state. These findings showed that, in unobstructed movements, the IC shifts and resulting shifts in the EP end approximately at peak velocity. In other words, during the latter part of the movement, the control signals responsible for the equilibrium shift remained constant, and the movement was driven by the arm inertial, viscous and elastic forces produced by the muscle-reflex system.

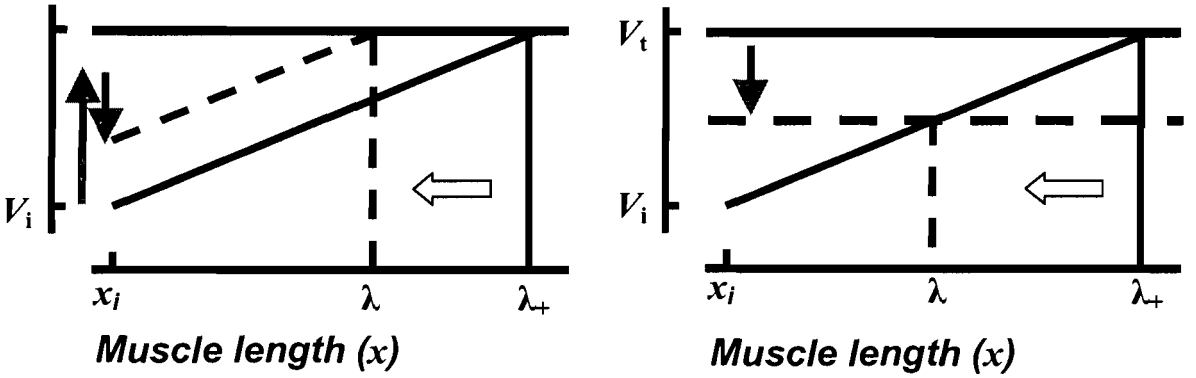
Threshold position control is a well-established empirical phenomenon that shows that motor actions and muscle activity emerge following resetting the threshold (referent) position of appropriate body segments, i.e. the virtual position at which muscles are silent but ready to generate activity and forces in response to deviations from this position (Asatryan and Feldman, 1965; Archambault et al. 2005; Foisy and Feldman 2006). Descending systems (cortico-, reticulo-, rubro- and vestibulo-spinal) can reset the threshold limb position (Feldman and Orlovsky, 1972; Nichols and Steeves, 1986). Such resetting is mediated by pre-, post-, mono- or poly-synaptic inputs to α- and/or γ- motoneurons (Matthews, 1959; Feldman and Orlovsky, 1972; Capaday, 1995). These control influences can be conveyed to motoneurons by all spinal neurons, including interneurons of reflex loops, for example, those influenced by group I and II muscle spindle afferents acting both mono- or polysynaptically on motoneurons.

1.2.4 Physiological origin of threshold position control

Motoneuronal activity is usually characterized by electrical units such as membrane potential or currents. When a muscle is stretched from an initial position x_i, the Ia afferent is increasing its discharge rate, and the motoneuronal membrane potential depolarizes and eventually reaches an electrical threshold V_t at which the motorneurons begin to be recruited. The muscle length, at this instance, is regarded as the threshold muscle length (λ+), Figure 1A. When independent control inputs are added (↑:depolarization, ↓:hyper-polarization), the same stretch elicits motoneuronal recruitment at a new threshold length (λ). A shift in the muscle threshold (λ) length can also occur by shifting the electrical threshold (V_t), Figure 1B (ref regarding experimental data). A change in

membrane potential precedes the generation of motoneuronal spikes that form EMG bursts underlying motor actions. A shift in threshold position is therefore initiated prior to the onset of EMG activity and force generation (feedforward process). Thus, the motoneuronal activity and therefore muscle EMG activity emerge due to a difference between the actual (x) and the threshold (λ) muscle length (Feldman et al. 2007).

The observations that the nervous system can modify the *threshold position* at which muscles become active imply that the electrical thresholds are somehow transformed into positional variables, thus *placing our actions in a spatial frame of reference associated with the body or with the environment.* Such a transformation can be explained by considering how proprioceptive and other sensory inputs are combined with independent, control inputs at the level of the membrane of motoneurons or other CNS neurons.



(A) (B)

Figure 1. Physiological origin of threshold position control. Each motoneuron (MN) receives afferent influences that depend on the muscle length (x) as well as on central control influences that are independent of muscle length. The MN is recruited when the membrane potential exceeds the electrical threshold (Vt). A: When the muscle is stretched quasi-statically from an initial length (xi) the motoneuronal membrane potential increases from its initial value (Vi) according to afferent length-dependent feedback (e.g. Ia fibers) from the muscle (solid diagonal line). The electrical threshold (Vt) is eventually reached at length λ+, at which the motoneuron begins to be recruited. When independent control inputs are added (↑:depolarization, ↓:hyper-polarization), the same stretch elicits motoneuronal recruitment at a shorter threshold length (λ). B: Shifts in the spatial threshold (horizontal arrow) can also result from changes in the electrical threshold (vertical arrow). In both cases (A or B), shifts in the membrane potentials and respective changes in the threshold position are initiated prior to the onset of EMG activity and force generation (a feed-forward process). Thereby, the activity of motoneurons and muscle force emerge depending on the difference between the actual (x) and the threshold (λ) muscle length. Reproduced with permission from Pilon et al. (2007).

1.3 Objectives

The review of literature shows that there is a great deal of controversy in the understanding of how goal-directed movements are controlled. The general objective of this study was to address this controversy. The specific objective of the study was to test the following prediction of the minimization rule in guiding goal-directed movements: Mechanical perturbations that delay the performance of one component of RTG movement postpone the appearance of other components. We conducted these experiments with perturbation applied to the wrist or trunk for two main reasons. First, we applied mechanical perturbation to the wrist at randomly chosen phases during reaching. This is a new perturbation method allowing us to test whether or not the minimization rule is valid for RTG movements. Second, we mechanically prevented trunk motion at the beginning in order to find how the hand transport and grasp aperture are affected and whether or not these two movement components are differently postponed.

Two experiments were conducted:

(1) The hand transport was blocked at the wrist level in RTG movements towards the object placed within the arm's reach (experiment 1).

(2) The trunk was blocked in RTG movements towards the object placed beyond the arm's reach (experiment 2).

CHAPTER II

2.0 Methods

2.1 Subjects

Healthy right-handed males and females (7 in experiment 1 and 7 different subjects in experiment 2; age of the group 34±10 years) participated in the study after signing informed consent forms approved by the Ethics Committee of the Center for Interdisciplinary Research in Rehabilitation (CRIR). Subjects were excluded from the study if they had some problems that affected their ability to produce RTG movements.

2.2 Experimental procedures

2.2.1 Perturbations of arm movements (experiment 1)

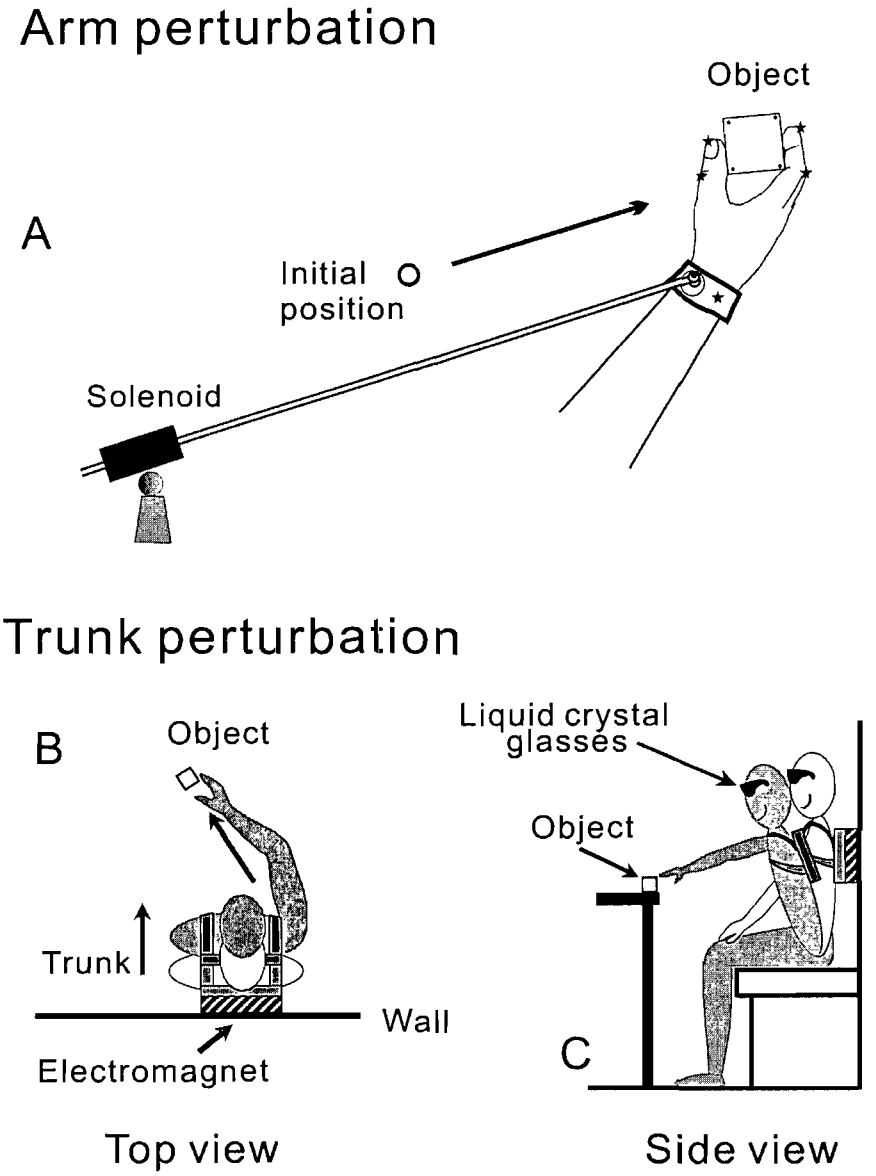


Fig. 2. Perturbations of reach-to-grasp movements made within (A) and beyond (B, C) reach of the arm. In A, subjects moved the arm from an initial position (open circle) to grasp, lift and place back a cubic object. A solid rod was attached to a bracelet on the wrist. When the arm moved, the rod was sliding inside a solenoid. In randomly selected trials, the solenoid was activated to clump the rod, thus blocking wrist motion for a chosen period. Asterisks on the fingers and dots on the object show positions of markers. In B and C, the same object was placed beyond the reach of the arm, and subjects leaned the trunk forward to reach the object. Before the onset of each trial, the electromagnetic plate attached to the back of the harness worn by the subject was locked to an electromagnet on the wall behind the subject. In most of trials, the electromagnet was unlocked simultaneously with the signal to move such that the trunk motion was not obstructed but in the randomly selected remaining trials the electromagnet remained locked, thus blocking trunk motion. Vision of the arm and object was available only before the signal to move and after the arm returned to the initial position.

Subjects were seated in a chair with a back support had to move the hand in order to grasp an object placed on a table within the reach of the right arm (Fig. 2 A).

The forearm and hand initially rested on the table. The starting position of the hand was indicated by a light-emitting diode embedded in the surface of the table and located about 20 cm in front of the sternum. The shoulder was slightly abducted and the elbow was flexed at approximately 90°. At this position, the pads of the index finger and the thumb touched each other. In response to a "go" signal (tone) from a computer, subjects quickly moved the hand from the initial position to a light cubic object (5x5x5 cm) located in the ipsilateral arm workspace within the arm's reach, about 80° from the sagittal midline, and about 35 cm from the starting position of the fingers, adjusted according to the subject's arm length. They had to reach for the object, grasp it with the index finger and the thumb, lift it 5-8 cm above the table and put it back. Two sides of the cube were approximately parallel to the hand path, making arm motion comfortable, grasping easy, and trunk involvement unnecessary.

In 40% of randomly selected trials, unknown to the subjects, the wrist motion towards the object was stopped by an electromagnetic device for about 200 or 400 ms at randomly selected phases of hand motion. The perturbation was delivered through a light but rigid plastic rod (1.4 m). One end of the rod was connected via a universal joint to a bracelet on the wrist of the right arm (Fig. 1 A). The rod could slide on bearings inside a cylindrical electromagnet (solenoid) that was attached via a universal joint to a vertical bar fastened to the table. When the electromagnet was off, the resistance of the rod to arm movement was negligible (*arm-free condition*). Activated by an electrical current, the electromagnetic device clamped the rod, thus preventing the wrist movement (*arm-perturbed condition*). The length of the rod was conditionally divided into 5 equal segments. A computer program randomly selected one of these segments

and thus the phase of arm motion at which perturbation was initiated. The time when the road was clumped was also randomly selected (200 or 400 ms). Because of mechanical delay in the electromechanical device, the actual clump duration of perturbation could actually vary about these values by 30-80 ms.

Subjects wore liquid crystal glasses (Translucent Technologies, Plato S2 Spectacles). They became opaque simultaneously with the "go" signal and blocked vision of the object and the arm. RTG movements were thus produced without vision, depriving subjects of knowledge of results and diminishing their tendency to make on-line corrections (Adamovich et al. 1998, 1999; Poizner et al. 1998). The glasses became transparent when the hand returned to the initial position.

No feedback regarding their performance was given to subjects. Subjects were instructed to make a single, smooth movement at a comfortable speed. There was a short rest period (5-10 s) between trials and 5-6 min between blocks of 20 trials (6 blocks in total). Movement did not require substantial learning since a short period of training (3-5 trials) with vision before the data collection onset was sufficient for subjects to produce required RTG movements without vision. During practice, no arrest of the arm was made but subjects knew in advance that perturbations will be made after the training session. They were instructed to make movement in the same way in each trial, whether or not the movement was perturbed, without trying to intentionally overcome the external resistance resulting from wrist arrest or make movement corrections. They also were informed that the wrist arrests will be made in an unpredictable manner and they should not anticipate the experimental condition in each trial.

2.2.2 Perturbation of trunk motion during trunk-assisted reaching (experiment 2)

Subjects were sitting on a stool with the right hand initially resting on the right knee and had to reach and grasp the same cube but placed in the contra-lateral workspace at the angle of about -40° from the sagittal midline, at a distance that exceeded the length of the fully stretched arm by about 15% (Fig. 2 B, C). Thus, to reach the object, it was necessary to lean the trunk forward (about 15-20 cm at the level of the shoulders). Subjects wore a harness with an electromagnetic plate fastened to the back surface of the harness at the level of the scapulas. Before the "go" signal in each trial, the plate was locked to a height adjustable electromagnet attached to the wall behind the electromagnetic plate. When locked, the electromagnet held the trunk in the initial, vertical position. In 40% of 180 trials, the electromagnet was unlocked simultaneously with the "go" signal so that trunk movement was unobstructed (free-trunk condition). In 40% of randomly selected trials the electromagnet remained locked for a randomly selected period (450, 600, 800, or 1000 ms from the "go" signal), thus blocking and then permitting trunk motion (blocked-trunk condition). Note that, in this experiment, only the perturbation offset was varied, unlike experiment 1 in which the perturbation onset was varied as well. In addition, for the same time of locking the electromagnet (say, 450 ms), the trunk arrest duration was smaller than that and varied depending on the reaction time to "go" signal. Based on preliminary tests, we found that arm-hand kinematics of RTG movements remained the same if the electromagnet was on less than 400 ms. The minimal time of locking electromagnet (450 ms) chosen in the present study was optimal in occasionally producing some or no effects on arm-hand kinematics in different trials (see Results). With 450 ms on-duration, the trunk arrests were terminated near the time when wrist reached its peak velocity.

The electromagnet was powerful enough to counteract the muscle torque resulting from the obstruction of intended trunk flexions. However, since this torque was transmitted to the harness via soft body tissues, there was small residual trunk motion (less than 5 cm at the level of the shoulder) in blocked-trunk trials. As in experiment 1, subjects practiced 3-5 trials (with vision, no perturbation). Instructions for this experiment were similar to those for experiment 1, except that subjects were not required to minimize the hand aperture before the signal to move.

2.3 Data recording and analysis

Movements were recorded using a 3D-motion analysis system (Optotrak, Northern Digital Inc., sampling rate 200/s). Markers (infrared light-emitting diodes, 8 markers in total) were placed on bony landmarks – the tips of the thumb and the index finger, the middle of thumb and index finger, the head of the ulna (wrist), lateral epicondyle (elbow), right and left acromion processes (shoulders), and sternal notch (trunk). Data were analyzed offline using customized LabView and MatLab software. The coordinates of the fingertips, wrist and sternal markers were used to compute, respectively, the hand aperture (distance between markers placed on the tips of the index finger and the thumb), wrist and trunk trajectories, as well as velocities (Adamovich et al. 2001). The object and its position were digitized during calibration of the 3D system.

Hand motion was characterized by the trajectories of three markers located on tips of the thumb and index finger, and on the head of the ulna (wrist). The hand aperture was characterized by the distance between the markers on the tips

of the thumb and the index finger. When the fingers' pads touched each other (zero aperture), the distance between the markers was about 2 cm. The measured distance was diminished by 2 cm to make it closely resembling the aperture size.

The finger plane was defined by 3 finger markers located on the tips of the index finger and thumb and in the middle of the index (Fig. 1 A). Unit vector (**n**) normal to this plane was determined as

$$\mathbf{n} = (\mathbf{V_3}-\mathbf{V_1}) \times (\mathbf{V_2}-\mathbf{V_1}) / \left| \mathbf{V_3}-\mathbf{V_1} \right| \cdot \left| \mathbf{V_2}-\mathbf{V_1} \right|$$

where $\mathbf{V_1}$, $\mathbf{V_2}$ and $\mathbf{V_3}$ are vectors defined by the coordinates of the 3 markers. The plane orientation was characterized by the change in the angle between this vector at each point of wrist trajectory and the initial vector ($\mathbf{n_0}$) at the movement onset. This angle was determined based on the scalar (dot) product of **n** and $\mathbf{n_0}$.

For data averaging, movements were aligned with respect to their onsets determined as the time at which wrist tangential velocity rose above 5% of its peak value (Adamovich et al. 2001). Three coordinates of respective markers were used to compute individual and mean (±SD) trajectories of wrist (ulnar marker) and trunk motion (sternum marker) as well as changes in the hand aperture. These trajectories in blocked-arm and trunk trials were compared with the respective trajectories from those in free-arm and trunk trials for from each experiment across all subjects. Since perturbations were directed in the frontal direction in experiment 1 and in sagittal direction in experiment 2, we also analyzed not only the entire wrist trajectory but also its frontal and sagittal components, respectively.

Figure 3 illustrates how temporal effects of wrist arrests were measured. When the wrist was arrested in experiment 1, the frontal component of the wrist velocity rapidly reached an intermediate maximum and then began decreasing to zero (Fig. 3). The time when this maximum was reached (resembling the reversal in the sign of wrist acceleration) was taken as the onset of the wrist arrest. A similar maximum occurred in the changes of the hand aperture. The interval between the two events was taken as delay in the aperture response to wrist arrest (*on-delay*). We also determined the time required for the hand aperture to reach a plateau after the onset of wrist arrest (point p in Fig. 3). Delay in the aperture reaction to the wrist release (*off-delay*) was determined as the interval between the renewal of the wrist motion (the time when the wrist velocity began to steadily increase and remained above zero for at least 50 ms) and the respective renewal of aperture changes. Similar criteria were used to determine off-delay in responses unblocking the trunk in experiment 2.

2.4 Statistical analysis

One way ANOVAs were used to assess the effects of perturbations as well as trunk arrest on the measured variables in each experiment for each subjects. Post hoc analysis were performed based on Neuman-Keuls test. For each subject, the mean values of kinematics variables (duration of movement, magnitude of wrist transportation and aperture changing) were compared between two condition (trials with or without perturbations). In each perturbed trial, the values of temporal characteristics (e.g., Fig. 3) measured for different movement components (hand and trunk transport and aperture changes) were compared by using the paired-samples t-test (for 2 segments) or ANOVA (for 3 segments).

Linear regression analysis and regression coefficients were used to evaluate coupling between different variables. Kinematics variables for the segment which was perturbed were independent variables, and those for the segment which was unaffected by perturbation were dependent variables. The level of significance of $p<0.05$ was used in all tests.

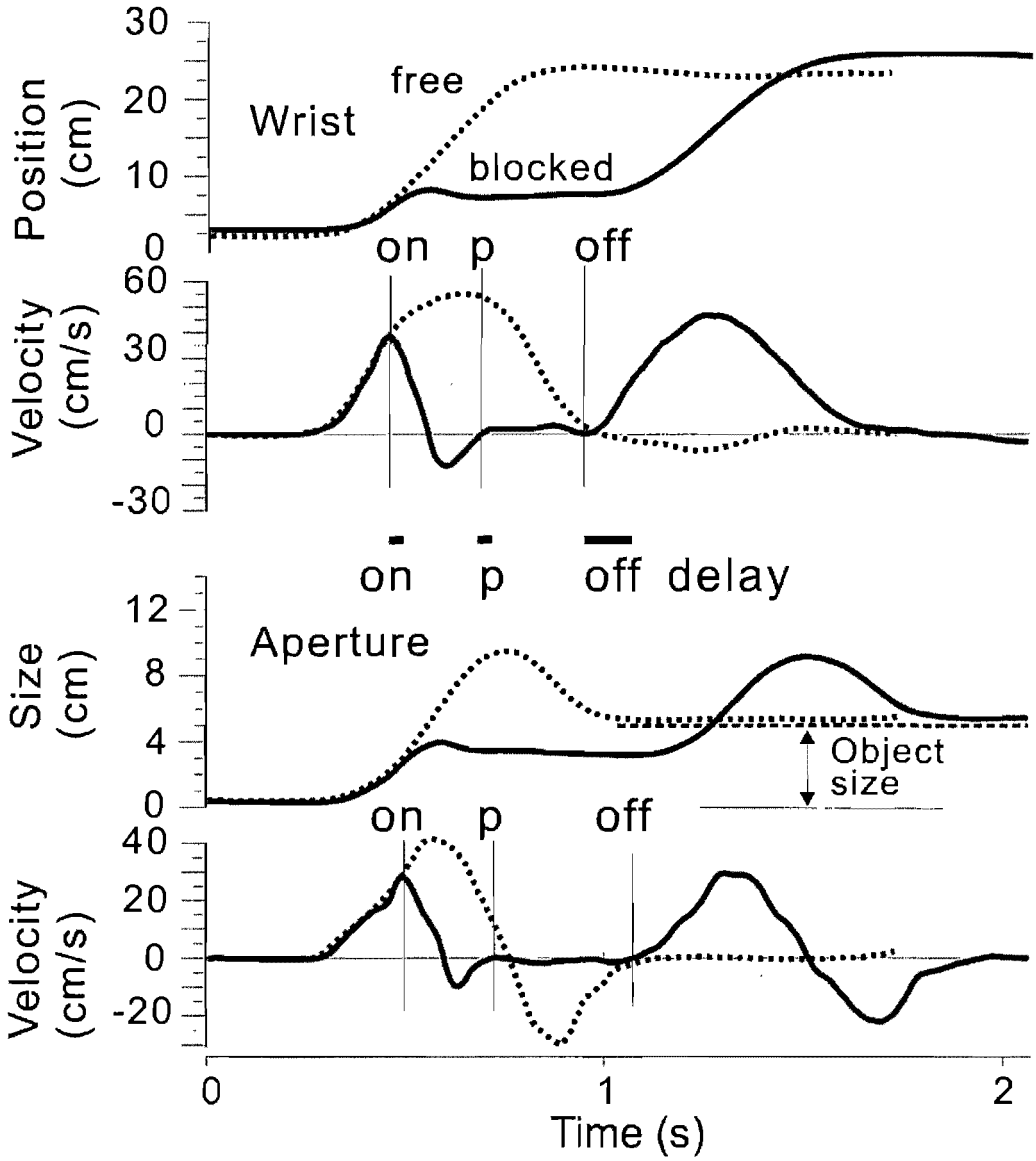


Fig. 3. An example of aperture reactions to wrist arrest in experiment 1. Vertical lines show the time when the wrist and aperture velocities begin to decrease in response to wrist arrest (on-points), reduced to zero (p-points) and began to increase again (off-points) after the wrist was unblocked. Recordings were taken from two sequential free-wrist and blocked-wrist trials.

CHAPTER III

3.0 Results

3.1 Arm arrests in reaching within the arm's reach (experiment 1)

Although vision was blocked before arm movement in each trial, all subjects had no difficulty in reaching and grasping in non-perturbed and perturbed movements. In very rare trials (1-2 trials per subject), grasping was unreliable such that the object was unintentionally dropped. These trials were excluded on-line and the respective number of trials was added.

Non-perturbed RTG movements had several characteristic features (Figs. 3-6). The hand and wrist smoothly moved directly towards the object whereas the hand aperture initially increased, to about 10 cm in Fig. 2 or to 8.7 ± 2.9 cm (mean ±SD) for the group, until it exceeded the object's size of 5 cm (opening phase) and then decreased (closure phase). In free-wrist trials, the movement time (from the hand movement onset to the time when the aperture velocity reached and stayed near zero level) was 1.18 ± 0.11 s (group values). Figure 4 A shows that, in free-wrist trials, the hand gradually rotated about the wrist flexion-extension axis by 26.7 ± 3.2° in the extension direction. During the closure phase, the hand rotation reversed by about 10°.

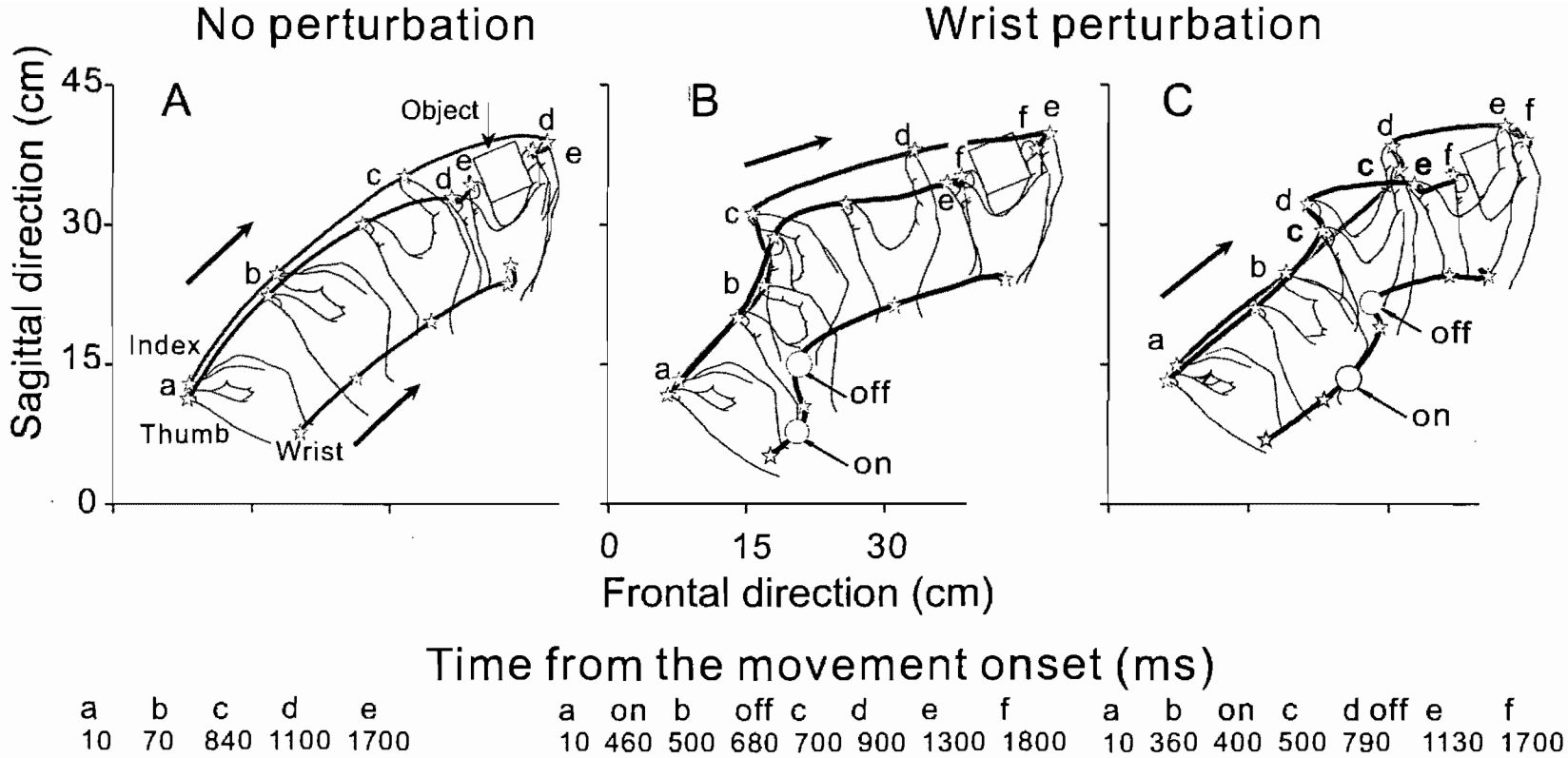


Fig. 4. Effects of wrist arrests on the wrist-hand configuration. Sketches show sequential positions (a-f) of the wrist and hand at different instances (listed below the panels) in sequential trials without (A) and with (B, C) wrist arrests initiated (on) and terminated (off) at different times after the movement onset. Two dark and one grey curves represent trajectories of wrist, tip of thumb and index finger respectively. Stars show corresponding markers.

Since perturbation was made by clamping the rod connected to the wrist via a universal joint (Fig. 2 A), only wrist motion in the direction towards the object was blocked, leaving the possibility of wrist rotation around the point at which the rod was clamped (rod radius about 1.4 m). In response to perturbation, the hand somewhat deviated from the non-perturbed path (Fig. 4 B, C), apparently due to an inertial rotation of the hand when the rod was clamped. The hand eventually stabilized in a new position 217 ± 72 ms after the onset of perturbation (group mean; determined as the interval between on- and p-points for the wrist graphs in Fig. 3). After the end of perturbation, when the target-directed arm motion resumed, the hand orientation gradually returned to that in trials without perturbation (Fig. 4 B, C).

We determined whether or not the total movement duration increased in proportion to the duration of wrist arrest. We distinguished between short-lasting (<300 ms) and long-lasting (> 300 ms) wrist arrests. The movement duration increased in proportion to the duration of the wrist arrest, in all subjects. Specifically, the movement duration differed for each pair of conditions (free-wrist, short-lasting, and long-lasting wrist arrests; group means: 1.18 ± 0.11 s; 1.42 ± 0.14 s; 1.64 ± 0.13 s, respectively; $p<0.05$ for the group as well as for each subject. e.g. comparison between the conditions of free-wrist and short-lasting wrist arrest for S1, $F(1, 90) = 25.82$, $P < 0.01$) resembling the difference in the duration of wrist arrests.

Changes in the hand aperture were also substantially affected by blocking wrist motion: the hand aperture ceased to change when the wrist was arrested, as illustrated by plateaus in the aperture curves in Fig. 3 and 5. By blocking wrist motion at different instances of reaching it was possible to discontinue changes in the hand aperture, practically at any time, not only during the opening (Fig. 5 A-D) but also during the closure phase (E). Figure 5 also show that changes in the aperture resumed only after the wrist was unblocked.

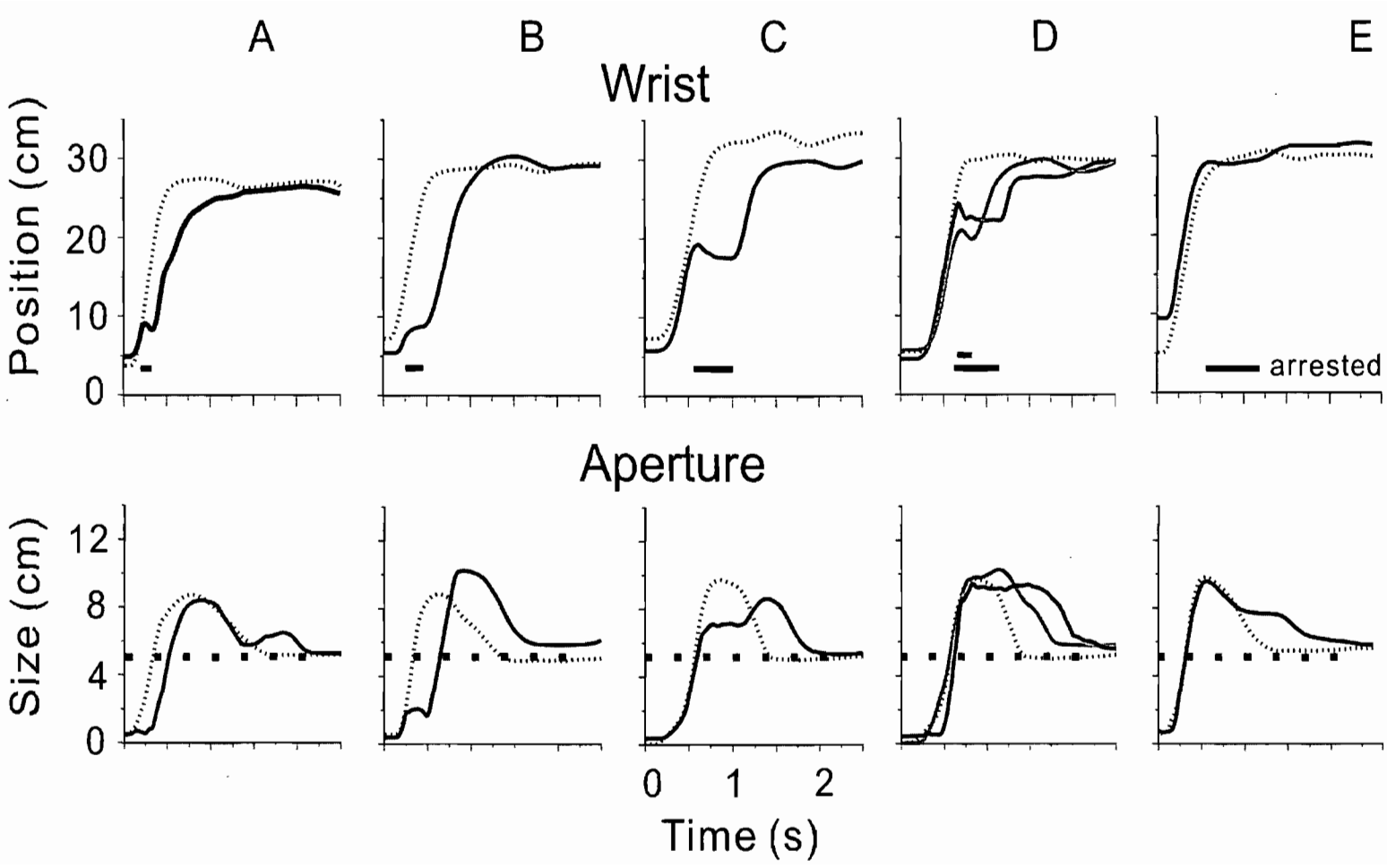


Fig. 5. Aperture changes could be halted practically at any phase by manipulating the onset and duration of wrist arrests (horizontal bars in the upper panels). Recordings from two (A-C, E, trials without perturbation prior to those with perturbation) or three (D, short-lasting perturbation happened prior to long-lasting perturbation) sequential trials for the same subject are shown. Solid and dashed curves show the wrist position and aperture size in trials with and without perturbation, respectively. Dashed horizontal lines in the lower panels show the object's size.

We determined delays in the aperture response to the onset (on-delay) and offset (off-delay) of wrist perturbation as defined in Fig. 3. For 5 out of 7 subjects, the on-delay was significantly smaller than the off-delay for individual subject (76 ± 60 versus 105 ± 55 ms; t-test, $p<0.01$. e.g. for S1, $t(92) = -14.84$, $p<0.01$). The changes in the hand aperture reached a plateau (p-delay in Fig. 3) 45 ± 67 ms after the wrist motion was fully halted. For 6 out of 7 subjects, p-delay was insignificantly correlated with the onset time or duration of the wrist arrest. Only in one subject, off-delay significantly correlated with the duration of wrist arrests, being shorter for long-lasting arrests.

The aperture plateau duration strongly correlated with the duration of wrist arrest, in all subjects. The slope of the regression line between these durations was close to 1 (range 0.975- 0.989 for all subjects). Because of delays involved in aperture responses to perturbations, the aperture plateau duration exceeded that of wrist arrest.

The total wrist transport distance after the wrist was unblocked differed insignificantly from that in free-wrist trials, for each individual and for the group of subjects. This also was the case for the major, frontal component of the wrist movement extent (23.1 ± 2.5 and 23.5 ± 2.5 cm in the free- and blocked-wrist trials, respectively, for the group). The maximal magnitude of the hand opening after the wrist was released, was also insignificantly affected by the perturbation (6.5 ± 2.5 and 7.4 ± 3.7 cm for free-wrist and blocked-wrist condition, respectively, ANOVA, $p>0.15$).

In 5 out of 7 subjects, the distance between the object and the wrist marker at the peak of hand opening (aperture closure distance) in arrested-wrist trials significantly differed, by 2-4 cm, from that in free-wrist trials ($P<0.05$ for each subject; e.g. for S1, $F(1,118) = 32.56$, $p < 0.01$).

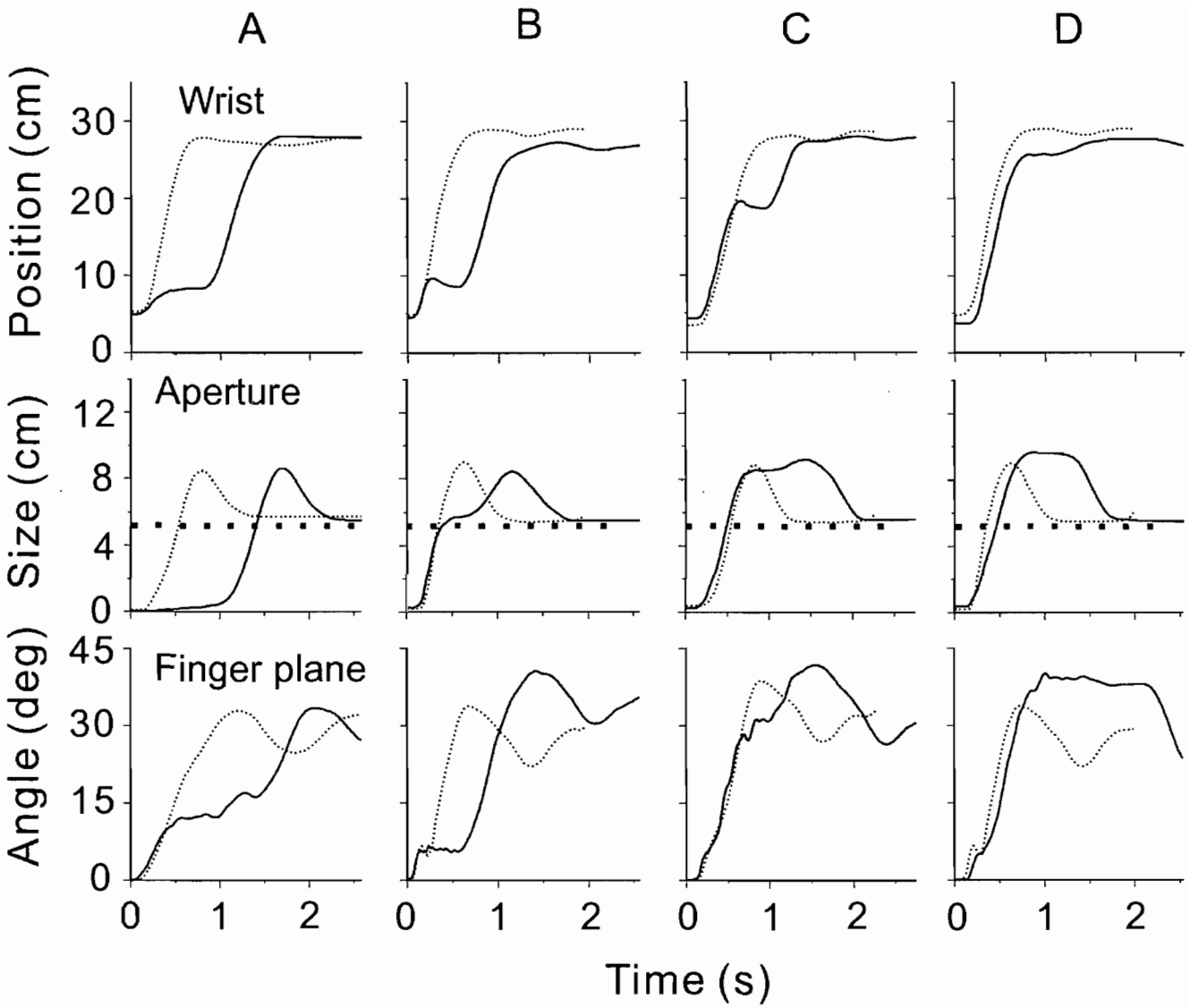


Fig. 6. Blocking wrist motion halted not only changes in the hand aperture but also in the rotation of hand. A-D show effects of wrist arrests initiated and terminated at different instances. Solid and dashed curves show changes in the wrist position, aperture size and inclination of a vector normal to the finger plane in trials with and without perturbation, respectively. Dashed horizontal lines in the middle panels show the object's size.

Although the RTG movements were made above the horizontal surface of the table, they were not planar. In particular, in trials without perturbation, subjects brought the hand several centimetres above and then lowered the hand to grasp the object. Another 3D-feature of RTG movement was that when the hand moved to the object, the finger plane rotated in the direction of supination by about 35° (Fig. 6, lower panels, dashed curves). When the hand was above the object, the finger plane inclination was diminished by about 10° such that, in the end of the transport phase, the fingers became optimally positioned for grasping. Like changes in the hand aperture, the finger plane rotation either substantially slowed down or completely ceased in response to the wrist arrest and resumed after the wrist was unblocked (Fig. 6, lower panels, solid curves).

To assess whether or not there was some adaptation in responses to perturbation in the course of the experiment, we compared the hand transport amplitude in the first and last 5 trials in the free-wrist and, separately, in the blocked-wrist condition. No significant differences were found for any subject. The hand aperture amplitude also differed insignificantly in the first and last 5 trials in either condition in 6 out of 7 subjects. In one subject, the aperture magnitude increased by about 4 cm from the initial 7 cm. Similarly, on- and off-delays insignificantly correlated with the number of perturbations experienced by the subjects from the beginning of the experiment.

3.2 Trunk arrests in reaching beyond arm's reach (experiment 2)

In experiment 2, subjects were required to reach and grasp the same cubic object as in experiment 1 but the cube was placed beyond the arm's reach. Therefore, to reach the object, subjects moved the trunk to overcome the limitation of the arm movement extent. Unlike experiment 1, subjects were not required to minimize the hand aperture before the movement onset and all of them kept the fingers opened before the signal to move such that the initial aperture was 1-2 cm smaller than the object's size (Fig. 7 – 9, dashed curves). In free-trunk trials, the wrist gradually moved toward the object while the aperture initially increased (opening phase) and then decreased (closure phase) to grasp the object. In the end of the opening phase, the aperture exceeded the object's size by the same amount in each subject, but this amount was different for different subjects – about 2.5-3 cm in subject S1 and S5; 5-6 cm in the other 5 subjects (Fig. 9, showing the results for S1- 4, lower panels, horizontal arrows).

Wrist motion and hand aperture could be affected or not by trunk arrests depending on the arrest duration. The minimal duration (450 ms) of trunk arrests in experiment 2 was chosen in such a way that these arrests were terminated at the time when the wrist reached its maximum speed, signifying the end of hand acceleration phase (see Methods and Fig. 7). Such arrests could influence the hand trajectory and aperture (Fig. 7; Fig. 9, curves 2 and 3 for subject S3) or just the aperture (Fig. 9 curves 2 for subjects S1 and S4). There were no cases when the duration of perturbation influenced only the wrist trajectory.

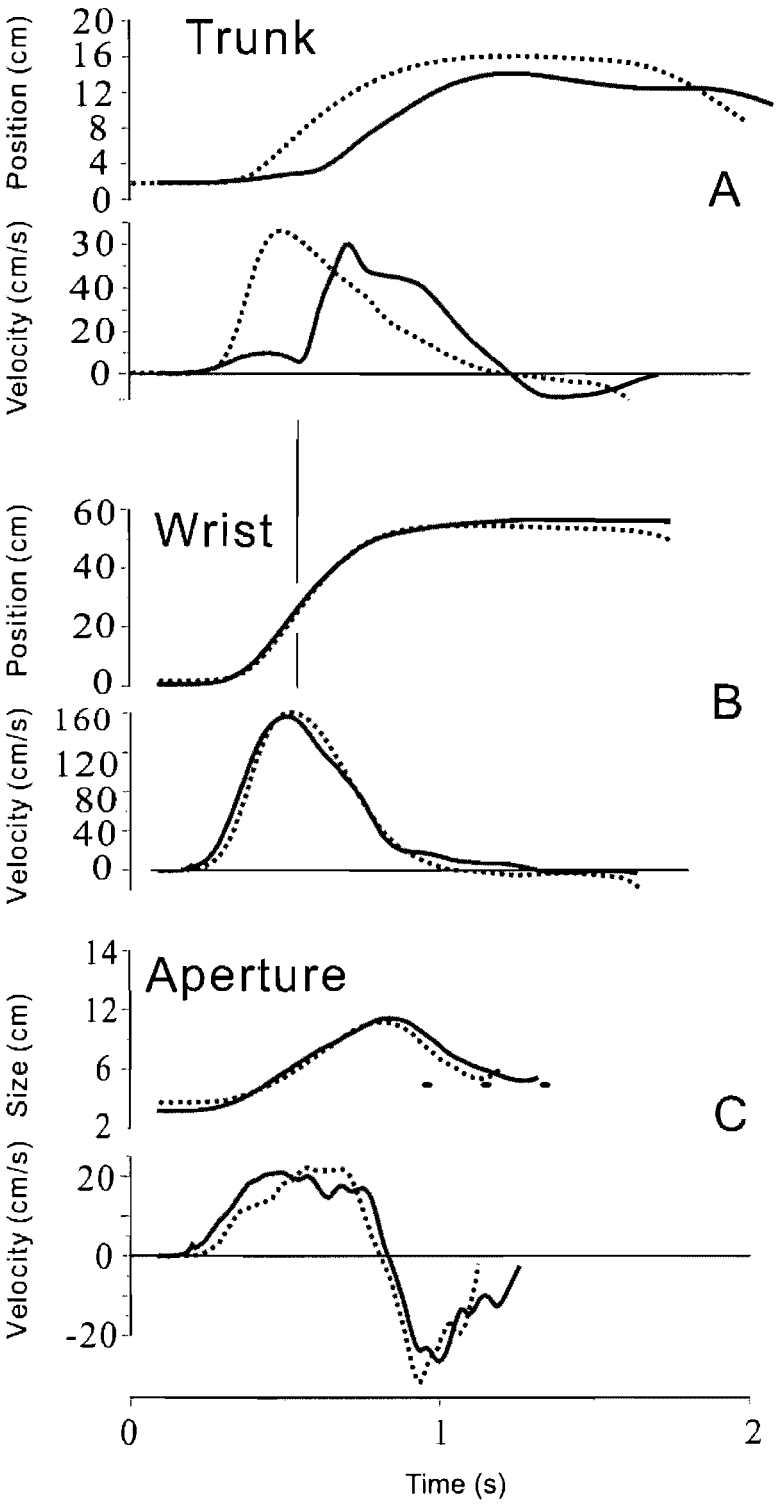


Fig. 7. The absence of wrist and aperture responses to a short-lasting (around 450 ms) trunk arrest terminated soon after the wrist reached its peak velocity (vertical line) in experiment 2. Solid and dashed curves show the trunk and wrist positions and the aperture size in sequential trials with and without perturbation, respectively.

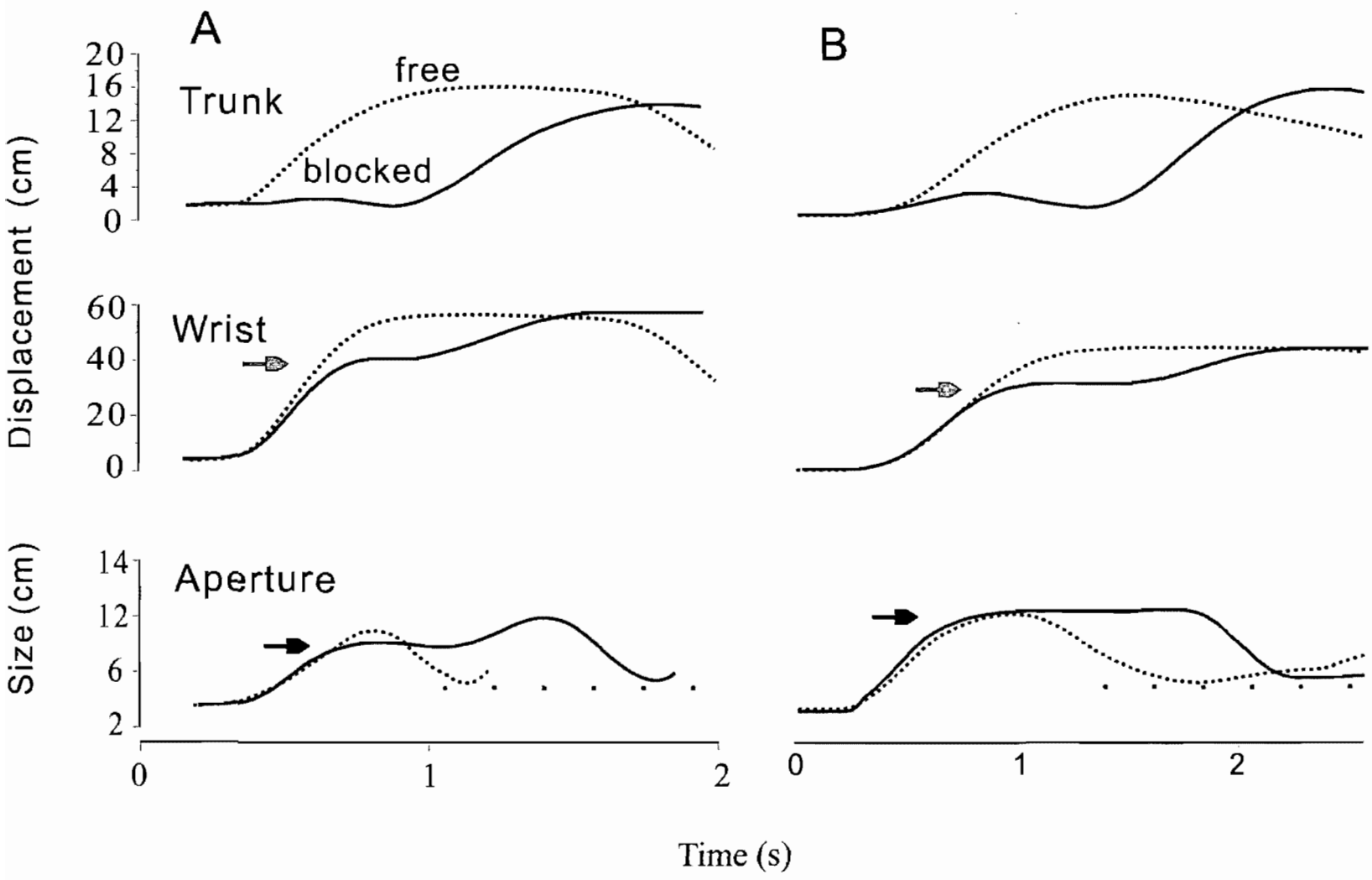


Fig. 8. Effects of prolonged trunk arrests terminated some time after the wrist peak velocity. Both changes in the wrist position and aperture were halted following such trunk arrests (horizontal arrows) but after substantial delays. After the end of trunk arrests, the wrist moved directly to its final position whereas fingers either resumed opening before closing (A) or, in another subject, began closing (B) on the object without resuming opening.

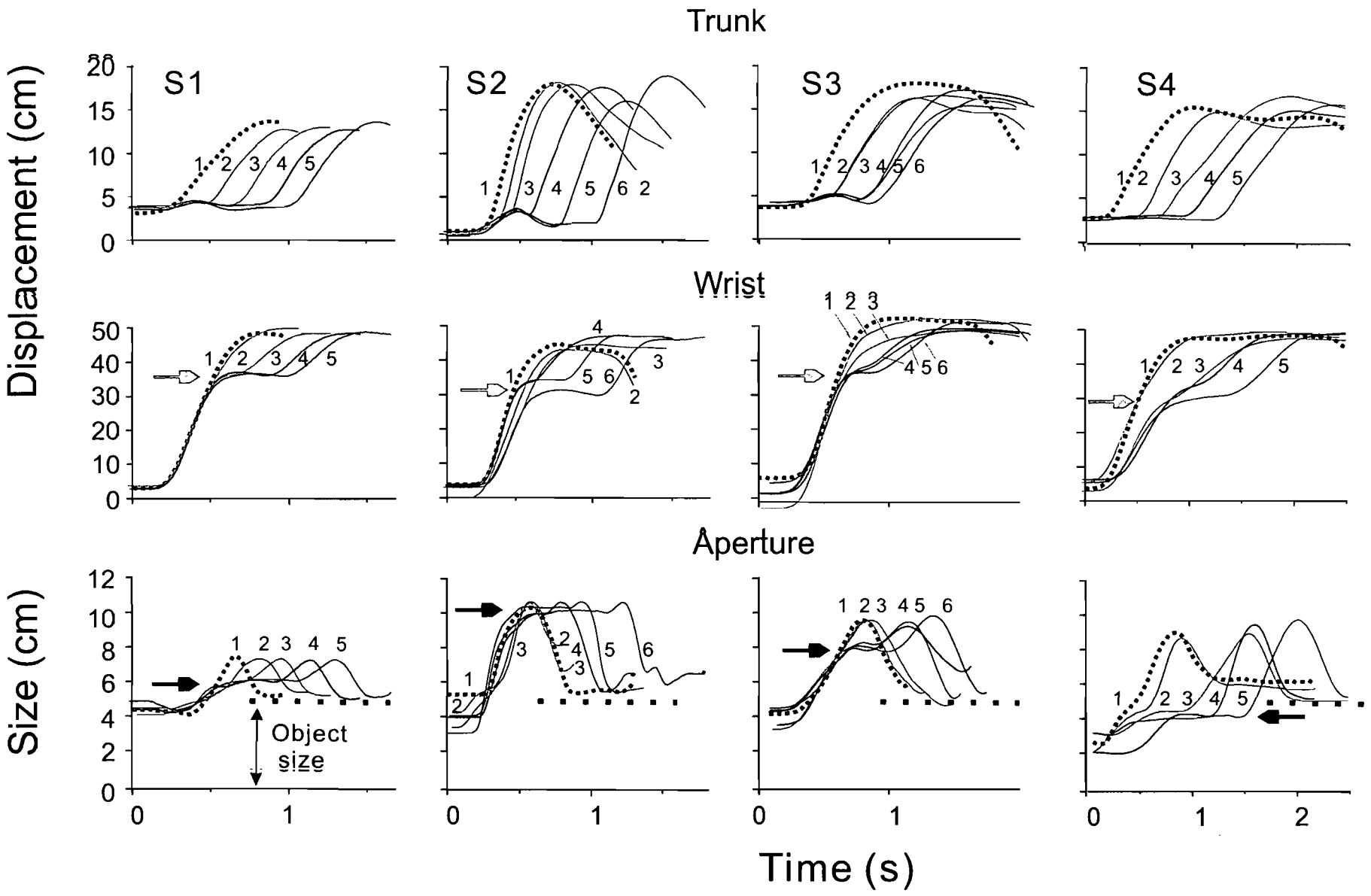

Trunk
Wrist
Aperture
Displacement (cm)
Size (cm)
Time (s)
S1
S2
S3
S4
Object size

Fig. 9. Effects of increased duration of trunk arrest on wrist motion and aperture in reach-to-grasp movements in experiment 2. Short-lasting trunk arrests (curves 2 in upper panels) could not influence the wrist motion and aperture (in S3) or could influence aperture only (in S1, S2, and S4). Both wrist motion and aperture were affected by prolonged trunk arrests (curves 3-6). Thereby, the wrist initially moved along the unperturbed path (dashed curves) but then reached an intermediate steady position (grey horizontal arrows in middle panels). The hand aperture changes were also halted at some phase of hand opening that was different for different subjects (black horizontal arrows). After the end of trunk arrest, the wrist motion and aperture changes resumed to eventually grasp the object.

Prolonged trunk arrests (> 450 ms) had no immediate effects on the wrist trajectory and hand aperture. These effects became apparent later, at about the time when the wrist reached its peak velocity (Fig. 8 and 9). Specifically, the wrist initially moved along a path coinciding with that in free-trunk trials but then diverged from it and arrived at a steady position at some distance from the object (without trunk motion, the full arm extension was insufficient to reach the object placed beyond the reach of the arm). After the trunk was unblocked, the wrist resumed motion to its final destination such that eventually the object was reached (Fig. 9, curves 3-5 in the middle panels).

Effects of prolonged trunk arrests on the aperture were also delayed: after the perturbation onsets, the aperture continued to increase as in trials when the trunk was not obstructed but then started to approach a steady size (plateau) that was eventually reached if the trunk arrest was sufficiently long (horizontal arrows in Fig. 8 and 9). The p-values characterizing the duration of reaching an aperture plateau in blocked-trunk trials in experiment 2 were substantially higher, than in blocked-wrist trials in experiment 1 (623 ± 68 ms for blocked-trunk versus 278 ± 73 ms, for blocked-wrist conditions, respectively, $p<0.001$ for each subject; e.g. for S1, $F(1, 454) = 6435$, $p<0.001$). In all cases, the aperture plateau in experiment 2 was reached 106 ± 82 ms before the wrist plateau (t-test, $p<0.001$). When the trunk was unblocked, wrist motion resumed before aperture changes (53 ±29 ms versus 89 ± 50 ms across all subjects), implying that there was a proximo-distal sequence of resumption of segment motion.

The height of the plateau reached during prolonged trunk arrests in different trials was independent of the arrest duration, in each subject ($p>0.05$). Figure 9 (black horizontal arrows, bottom panels) shows that the height of the plateau was different for different subjects ($F(6, 168) = 2134$, $p<0.001$), it exceeded the object size by about 1-1.5 cm in 2 subject, by 4.5-5 cm in the other 4 subjects and was just below the object size in one subject (in Fig. 9).

When the trunk was unblocked, the finger movement resumed opening before closing on the object, in 6 out of 7 subjects (S1, S3, S4; Fig. 8 A; Fig. 9). The maximal aperture size reached before the closing onset insignificantly differed from that in free-trunk trials for each subject (Fig. 9, bottom panels). In one subject (S2 in Fig. 8 B and Fig. 9 for S2), the fingers began closing right after the trunk release or after a small secondary opening.

Trunk arrests interrupted changes not only in the hand aperture but also in the finger plane rotation if the trunk arrests were sufficiently prolonged (>450ms). The finger plane rotation reached a plateau in about 61 % of cases for the group. After the trunk was unblocked, the finger plane rotation and changes in the hand aperture resumed after about the same delay for each subject (t-test, $p>0.3$).

The aperture closure distance significantly differed among free-trunk, short-lasting and long-lasting arrested-trunk conditions for 1 out of 7 subjects ($p<0.01$, $F(2, 175) = 18$). The subsequent post-hoc analysis showed this closure distance was not different for short- and long-lasting trunk arrests ($p>0.05$), but bigger in free-trunk condition by 1 cm

Like in experiment 1, the aperture plateau duration strongly correlated with the duration of trunk arrests ($p<0.01$, range of slopes: 0.87 - 0.98). Delays in the re-initiation of wrist motion and hand aperture changes were independent of the perturbation duration. Wrist and aperture off-delays were not correlated. These delays were also not correlated with the number of perturbations (or total number of trials) experienced by subjects, and showed no signs of adaptive changes in response to perturbation.

CHAPTER IV

4.0 Discussion

4.1 Basic findings

When wrist motion was mechanically blocked in RTG movements towards the object placed within the arm's reach (experiment 1), the changes in the hand aperture ceased after delay of about 76 ms and resumed only after the wrist was unblocked, after delay of about 105 ms. By choosing appropriate latency of perturbation, one could interrupt aperture changes practically at any phase, not only prior to but also after the fingers began to close on the object.

When trunk motion in experiment 2 was prevented for relatively short time such that the trunk was unblocked when the wrist displacement approached or has reached its peak velocity, the hand and aperture responses to trunk arrests could occasionally be either present or absent in different trials. If present, both the wrist trajectory and aperture or the aperture alone was affected.

Prolonged trunk arrests made reaching the object mechanically impossible such that when the arm became maximally extended, the hand stopped moving at some distance from the object. When the trunk was released, the hand motion resumed (after delay of about 51 ms) and the object was eventually reached. Although the hand aperture was not mechanically constrained by the trunk and

hand motion, it also ceased to change when the trunk was blocked, even before the wrist ceased to move. The steady aperture size was maintained for about 111 ms after the onset of trunk release. In each subject, this steady size (a plateau height in the aperture curves) was the same for different durations of trunk arrests but was different for different subjects. Taken together for the group of subjects, these steady aperture sizes resembled two different phases of finger opening, from the phase when the plateau height was below the size of the object to that when the finger opening was maximal.

There was no sign of adaptive changes in responses to perturbations during the experiments.

4.2 Explanation of results based on the minimization rule

Different hypotheses were formulated on how RTG movements are produced. Some studies suggested that the grasp and transport components are temporally coupled (e.g., Jeannerod 1981, 1984; Paulignan et al. 1991a; Marteniuk et al. 1990; Hoff and Arbib 1993; Bootsma et al. 1994; Timmann et al. 1996; Rand et al. 2000; Smeets and Brenner 1999; Wallace and Weeks 1988; Wallace et al. 1990). Other studies suggested that they coordinated spatially, rather than temporally (e.g., Haggard and Wing 1991, 1995, 1998; Wang and Stelmach 1998, 2001; Saling et al. 1998; Rand et al. 2004; Rand, Smiley-Oyen et al. 2006; Alberts et al. 2000, 2002). Our study addresses this controversy.

Mechanical perturbations applied to the hand transport in our study differed from those in previous studies (Haggard and Wing 1995; Paulignan et al. 1991; Rand et al. 2004) in two ways. First, In our study, perturbations stopped the wrist or trunk motion, instead of pulling or pushing the arm in the studies cited above This allowed us to investigate both temporal and spatial effects of perturbation. Second, perturbation could be delivered at any phase throughout the movement and could be varied in terms of duration.

In experiment 1, the perturbation blocked wrist in the direction to the object, leaving the wrist rotation in other directions unaffected. Following the perturbation, hand aperture changes and finger plane rotations were interrupted and resumed soon after the wrist was released. This finding confirmed the prediction of the minimization hypothesis that different movement components are interdependent such that interruption of one movement component postpones the performance of the other component.

The finding that changes in the hand aperture and wrist rotation could be interrupted and resumed practically at any phase of motion implies the unperturbed movement components were all dependent on afferent feedback on line. In other words, the grasp component should not be considered as a fully pre-programmed action. Even the closure phase of the grasp, when the hand transport has almost completed, can be interrupted, implying that the grip aperture could not be considered as independent of afferent feedback (Jeannerod, 1981, Jeannerod et al., 1984; Jeannerod et al., 1995).

Such immediate temporal and spatial responses of hand transport and aperture to the perturbation did not appear in experiment 2. Instead, wrist motion and aperture changes were affected after substantial delay and only if trunk arrests were sufficiently prolonged. When the object is beyond the reach, the wrist extended to its limit and the aperture increased to a certain size regardless of the

trunk arrest. Since the trunk block made it is impossible to reach the object, the hand aperture was interrupted when it achieved a certain size. The invariance of hand trajectory is maintained by excluding the compensatory arm-trunk coordination (see below). When the trunk block was prolonged, the changes in wrist extent, hand rotation and hand aperture all appeared to deviate from those of free trials noticeably and substantially (remote effects of trunk arrests). These kinematic variables maintained the values that they achieved when they were interrupted. When the trunk was released, the changing in hand trajectory, hand aperture and wrist rotation began to rapidly merge with that of free-trunk trials after delays. These patterns suggest that the reaching and grasping components are coupled such the whole RTG movement is controlled as a single, coherent unit.

In experiment 2, the wrist velocity peak in free trial was insignificantly different from the first velocity peak in blocked-trunk trial. This is consistent with results of study by Rossi et al. (2002). When the trunk was involved to reach the target beyond the arm's reach, the trunk started moving together with the hand. However, the influence of the trunk motion on the hand trajectory was initially fully neutralized by appropriate changes in the arm joint angles (compensatory arm-trunk coordination). Only when the arm approached its extension limits, the degree ("gain") of compensatory arm-trunk coordination was attenuated to allow the trunk to contribute to the hand extent. The previous finding (Aadmovich et al. 2001) that, in trunk-assisted arm movements within the arm's reach, the hand trajectory remained invariant when the trunk was involved intentionally or mechanically blocked can also be explained by the same compensatory arm-trunk coordination that neutralize the influence of trunk motion on the hand position. In other words, although the arm and trunk initially moved simultaneously, they influenced the hand extent sequentially.

Long-lasting trunk arrests in experiment 2 postponed the contribution of the trunk neuromuscular system to reach the target. However, the last phase of hand movement after the trunk release was similar to that in free condition, in which the trunk contribution influenced the hand extending only after the arm reached its limit. The final part of aperture changing was also resumed following the trunk release, emerging with that of the free trials. Therefore, long-lasting trunk arrests, not only elicited hand movement undershoots but also interrupted a terminal part of the opening phase or the onset of the closing phase, as observed in the present study.

When the trunk was blocked, the wrist extent was not affected until a critical time, approximately, at peak velocity of the wrist transport. This finding confirmed the study of Ghafouri and Feldman (2001). Their study evaluated the duration of shifts in the equilibrium (referent) position of the hand underlying fast point-to-point arm movements. When the movement was prevented, the hand force and joint torques reached a steady state after a time that was much smaller than the movement duration and was approximately equal to the time to peak velocity of unobstructed movements. Based on this result, one can suggest that the peak velocity in our experiment 2 resembles the time when the control of RTG movement including the aperture component is transfered from the arm to trunk control system. This also explains why the effects of trunk arrests on the wrist trajectory and aperture were postponed: until the arm control system has accomplished shifts in the referent arm configuration, the trunk contribution to the hand movement extent was prevented by compensatory changes in the arm joint angles (Rossi et al. 2002) and only after this the trunk began to contribute to the hand movement extent whereas the aperture became dependent from trunk, rather than arm motion. Thus, the results confirm the predictions of the minimization rule on the possibility of halting aperture changes both in movement within (experiment 1) and beyond (experiment 2) arm's reach. Fig. 10 illustrates these

phenomenon: arm and trunk contributed to the hand transport sequentially; wrist trajectory and aperture changing for prolonged arrested-trunk condition diverged from those for free-trunk condition at a time that was approximately equal to thetime to peak velocity of unobstructed movements.

In several studies there is a tendency to give a priority to either spatial or temporal aspects in the control of RTG movements (Jeannerod 1981, 1984; Paulignan et al. 1991a; Marteniuk et al. 1990; Hoff and Arbib 1993; Bootsma et al. 1994; Timmann et al. 1996; Rand et al. 2000; Smeets and Brenner 1999; Wallace and Weeks 1988; Wallace et al. 1990; Haggard and Wing 1991, 1995, 1998; Wang and Stelmach 1998, 2001; Saling et al. 1998; Rand et al. 2004, Rand, Squire et al. 2006; Alberts et al. 2000, 2002). The minimization rule does not give a priority to one of these aspects, but rather considers them as mutually related. Specifically, it suggests that these movements are primary guided by a global factor that related to a spatial aspect of the motor action – the difference between the referent body configuration specified by the brain and its physical configuration emerging following the interaction of the neuromuscular elements between themselves and with the environment. This interaction is another global factor that implies how the control process is evolves in time. Therefore, implies that spatial and timing aspects of movement control are harmonized such that no priority can be given to one of them.

Wang and Stelmach (2001) showed that the distance to the target at which the hand closure is initiated (aperture closure distance) remains relatively invariant across different task conditions – changes in the hand movement extent or degrees of trunk involvement into RTG movement – but significantly depends on the amplitude of peak aperture, as well as hand velocity and acceleration (Rand et al. 2006). Our study further shows that the closure distance may be task- and condition-dependent. Indeed, these findings support the notion, inherent in the minimization rule, that spatial conditions – the appropriate hand movement

extent, sufficient opening and appropriate shape define when the closure phase starts.

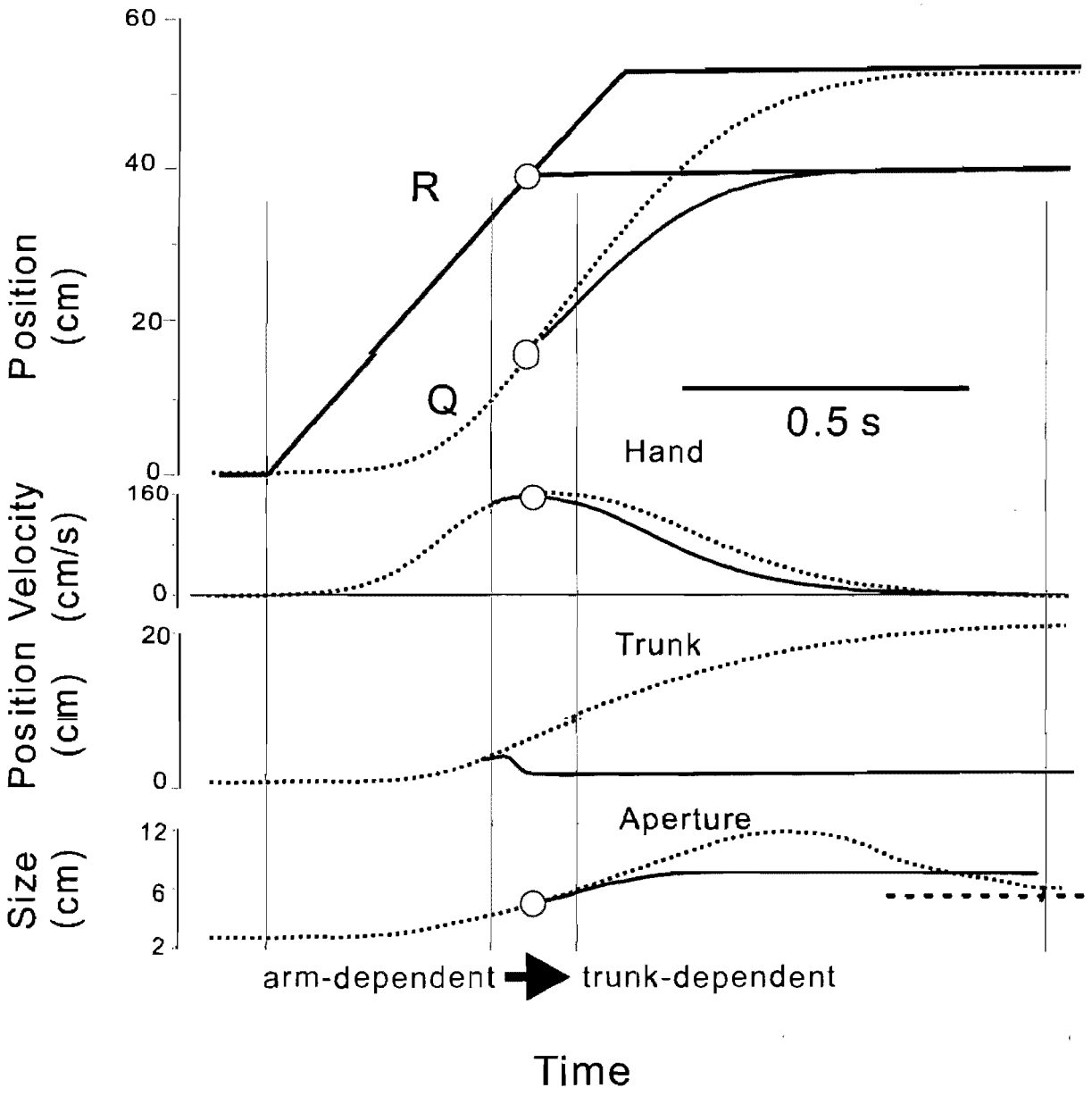


Fig. 10. A diagram of basic events underlying the control and production of reach-to-grasp movements beyond the arm's reach. It is assumed that, to elicit such a

movement, the nervous system gradually changes the referent arm configuration such that the referent position of the hand (R, thick solid ramp, upper panel) is shifted toward the object. Changes in the actual position of the hand (Q, dotted curve), trunk and aperture emerge following the tendency of arm and hand muscles and afferent feedback to minimize the difference between the actual and the referent arm-hand configurations. The arm control system has a priority in executing its control function first so that the influence of the trunk motion on the hand movement is initially neutralized by appropriate compensatory modifications of arm joint angles (Rossi et al. 2002). The arm control system shifts the R until it reaches a value representing an almost full arm extension. This occurs at a point (open circles) when the hand approximately reaches its peak velocity (Ghafouri and Feldman 2001). Until this point, the aperture changes are coupled to arm motion (arm-dependent). After this point, the compensatory modifications of arm joint angles cease, allowing the trunk to contribute to the hand movement extent. Respectively, the aperture changes become coupled to the trunk motion (trunk-dependent). The effects of prolonged trunk arrests halting the hand transport and aperture changes (thin solid lines), are straightforward consequences of this control strategy. Vertical lines separate three major phases in the control of reaching beyond the arm's reach: the initial phase when both the hand transport and aperture changes are guided by the arm control system, a final phase when these are guided by the trunk control system, and a transitional ("critical") phase when the control function is relayed from one to the other system.

4.3 The latency of responses to perturbations of RTG movements

Latencies of responses to perturbations were observed when the perturbations were on and off, both in experiment 1 and 2. In experiment 1, latencies of the interruption and resumption of changes in the hand aperture (76 and 105 ms, respectively) showed that the on-delay was shorter than the off-delay. The difference in the on- and off-delays in experiment 1 might be related to the difference in the mechanical stimulus that caused by perturbations: arm arrests apparently are more abrupt stimuli than arm releases. Respectively, the on-delay in reflex responses to wrist arrest could be smaller than to the off-delay. However, our results do not rule out the possibility that the difference in on- and off-delays reflect the difference in the central mechanism responsible for the initiation and termination of different movement components.

In experiment 2, trunk arrests and releases elicited not only proprioceptive responses, but also vestibular responses. it has been shown that, in arm movements within the arm's reach, vestibular responses play a major role in compensatory changes of the arm joint angles to keep the hand transport invariant regardless of whether or not the trunk is involved (Raptis et al. 2007). The latencies of wrist and aperture responses to trunk release (about 51 and 111 ms, respectively) are in the range of latency of vestibular responses to mechanical perturbations (Raptis et al. 2007). However, we cannot rule out the involvement of additional, spinal and supra-spinal pathways. The difference between the latencies of wrist and aperture resumptions may be related to the differences in motor unit recruitment in proximal vs. distal muscles. The sequence of reinitiating the hand transport and aperture changes implies that there was a proximo-distal sequence of involvement of different arm segments in motion.

To respond to perturbations, subjects might try to trigger some adaptive changes in central commands to the arm muscles although perturbations in all experiments were applied in relative rare trials (30% randomly selected trials). Such triggered reactions are usually issued comparatively late after the onset of

the perturbation (typically after 150 ms, e.g. Crago et al. 1976; Adamovich et al. 2002) and can easily be detected as a deviation of the hand trajectory from that in non-perturbed movements (Adamovich et al. 2002). To overcome the perturbation, subjects can use some anticipatory adaptive strategies that can be detected by analysing the changes in the latency of the resumption in sequential test trials from the onset of the experiment. If this is the case, latency of resumption in hand aperture components would be shorter when the numbers of trials subject had performed were bigger. According to the insignificant finding of our correlation analysis between the latency of aperture changing resumption and the trial numbers for both experiment 1 and experiment 2, on-and off-delays remained the same during the experiment, suggesting that adaptive reaction were minimised in our study.

4.4 Alternative explanations

It has been originally suggested (Jeannerod, 1981; Jeannerod et al., 1984; Jeannerod et al., 1995) that the hand transport and grasp components of RTG movements are pre-planned as separate units coordinated by a loose temporal coupling. In our experiment 1, the changes in the hand aperture were halted in response to wrist arrests and resumed after the wrist was released, showing that the hand aperture component depends on afferent feedback. Similar afferent dependent reactions were observed in experiment 2 in which the trunk motion was prevented, if the trunk arrest was sufficiently prolonged. In this case, the hand transport and aperture changes initially matched those from the free-trunk trials and then deviated from those when the hand reached its peak velocity. Hand transport and aperture resumed sequentially after delays when the trunk was released. Our results showed that different movement components are interdependent, following intersegmental afferent feedback, as was also the cases

in several previous studies (Wang and Stelmach, 1998; Wang and Stelmach, 2001; Jakobson and Goodale, 1991; Chieffi and Gentilucci, 1993; Wing et al., 1986; Haggard and Wing, 1991, 1995; Haggard and Wing 1998; Wang and Stelmach 1998, 2001; Saling et al., 1998; Rand et al., 2004, 2006, 2007; Alberts et al., 2000, 2002). Therefore Jeannerod's hypothesis must be modified to explain these results by integrating the following points. First, each movement component is dependent on afferent feedback. Second, each movement component represents a gradual, rather than a step-like process. Third, it should be more specific in terms of definition of spatial relationship between different components (modulus). Four, all components of RTG are interdependent.

CHAPTER V

5.0 Conclusions

The finding that changes in the hand aperture can be interrupted at any phase by arresting the wrist or trunk is consistent with the minimization hypothesis. The same hypothesis helps explain why the trunk arrest in experiment 2 influenced the hand aperture but not the hand transport. It has been previously shown that the contribution of trunk motion to the hand movement extent in motion beyond the reach of the arm is initially neutralized by compensatory changes in the arm joint angles until the hand transport reaches its peak velocity. Therefore, trunk arrest until this moment could not influence the hand transport. Changes in the hand aperture critically depended on whether or not the trunk motion could eventually bring the hand to the object, such that prolonged trunk arrest discontinued the aperture changes.

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